ANALYSIS OF SELECTION PRESSURES ACTING ON THREE POPULATIONS OF THE WINKLE LITTORINA RUDIS (MATON), AND THEIR EFFECTS ON LIFE-HISTORY TACTICS

by

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" How much of the acclimatisation of species to any particular climate is due to mere habit, and how much to the natural selection of varieties having different innate constitutions is an obscure question..."

C. Darwin

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INTRODUCTION

The synthesis of Darwin's (1872) theory of Natural Selection and Mendelian genetics (Fisher, 1930), has resulted in the idea that the gene is the unit of selection. Genes are 'selfish' in that their aim is to produce as many copies of themselves as possible; the individual exists only as a 'survival machine' (Dawkins, 1976). However, the usual way that genes produce more copies of themselves, is by co-operating together to induce their 'survival machine' to produce the maximum number of surviving offspring (but see Doolittle and Sapienza, 1980). Those genes which cause their 'survival machine' to be less well adapted to the environment, so that fewer surviving offspring are produced, will generally be selected against.

The way that each individual maximises its reproductive output is called its reproductive, or life-history, tactic. The life history tactic of each individual is the result of particular selection pressures acting upon it. In some circumstances it may be advantageous to produce a few young over a long period (e.g. elephant Loxodonta africana); in others it may be better to produce many young in one brief 'burst' (e.g. salmon Salmo salar). Other characteristics of an individual, e.g. size, growth rate, also a product of selection, may or may not be closely correlated with its reproductive tactics.

Life history tactics, and other characteristics, are measured using populations, rather than individuals, as differences between life stages, and individual variation, can then be compared. If two populations become geographicall isolated from one another, so that there is little gene flow between them, they may come to differ in reproductive, and other characteristics (Tamarin, 1978). This step is the first in the process of speciation (Dobzhansky, 1977). If the populations become sufficiently different, then subsequent breakdown of the geograph ical barrier may lead to the evolution of two distinct, sympatric species. Even if the two isolated populations differ only in their reproductive tactics, two distinct species could still be formed (e.g. charr Salvelinus alpinus, Frost, 1965). Differences evolved between two isolated populations will primarily be a result of different selection pressures acting upon them. Therefore, by examining characteristics of each population, and relating them to environmental

conditions, selection pressures important to each population can be inferred.

In this project, I attempted to detect and analyse selection pressures acting on three populations of the winkle Littorina rudis (Maton), by both inferring selection pressures from reproductive and other characteristics, and by field experiments.

Littorina rudis (Maton) was first described by Heller (1974), who separated the L.saxatilis (Olivi) aggregate into four sympatric species; Littorina rudis, L.patula (Jeffreys), L.nigrolineata (Gray) and L.neglecta (Bean). That L.patula is synonymous with L.rudis has been shown by Raffaelli (1979a). Recently a new species, L.arcana, has been described by Hannaford Ellis (1978, 1979).

L.rudis is the most widespread and abundant of the above species. It is found along the channel coast of Europe and extends into the Mediterranean as well as to Norway, Greenland, Iceland, Canada and the United States. Though characteristically an upper-shore species, its distribution is variable, and in some habitats may extend down to Mean Low Water Neap Level (MLWNT) (Emson & Faller Fritsch, 1976).

L.rudis is ovoviviparous, that is, embryos develop in the female's brood chamber, and are born as shelled young (Heller, 1974). There is no evidence that the female provides nutrients for developing young (Raffaelli, 1976). The number of embryos in the brood pouch follows an annual cycle, with high numbers through spring till May, falling markedly during the summer to recover in August (Berry, 1961; Raffaelli, 1976). Ovulation appears to be a continuous process, so that young at all stages of development are present in the brood pouch (Berry, 1961). Ovoviviparity may have evolved as a response to the desiccating effects of the upper shore. Retaining eggs in the brood chamber rather than laying them in masses on the shore (as in L.nigrolineata, Raffaelli, 1976) prevents loss at this stage. Elimination of the planktonic stage may also be a strategy for coping with reproductive uncertainty (Fo: theringham, 1971). In winkles which inhabit a very varied, heterogenous habitat, the absence of planktonic dispersal, and production of offspring which remain near the parent, may result in a population becoming adjusted rather precisely to local environmental conditions, (Heller, 1974). Electrophoretic studies on two polymorphic enzymatic loci of L.rudis,

have shown that significant genetic differentiation may occur over distances as little as 2 km (Snyder & Gooch, 1973). Therefore L.rudis is a species which can become separated into genetically distinct populations, each responding to the particular selection pressures acting upon them. These selection pressures are related to their habitat.

On cliff faces and large boulders, dislodgement by wave action and desiccation appear to be important selection factors (Raffaelli and Hughes, 1978). Crevices in the rock face provide refuges from both these mortality factors. Emson & Faller Fritsch (1976) have shown that populations of L.rudis are limited by the availability of crevices. When they drilled artificial crevices in large boulders, the density of winkles increased. They also found that as the number of empty barnacles increased, the number of small winkles that use barnacles as refuges increased. Similarly, Raffaelli & Hughes (1978) showed that shore level changes in size frequency of winkles correlates with changes in crevice widths. Large individuals are selected against on exposed shores if crevices are small.

Particularly violent wave-action may lead to selection for increased foot strength and area. Heller (1975) has demonstrated a cline in shell shape, from small, globose, wide-mouthed shells on exposed shores, to large, thin, narrow-mouthed shells on sheltered shores. A larger foot muscle can be accommodated in a wider-mouthed globose shell. On sheltered shores, narrow-mouthed shells are favoured as they discourage crab predation, large crabs being abundant mainly on sheltered shores. However, crab predation is minimal on muddy shores (Raffaelli, 1979), thus factors other than crab predation must maintain shell shape on these sheltered shores.

The same traits in shell shape have been found by Newkirk & Doyle (1975), who showed that, in all populations studied, the additive genetic variance of aperture size and 'globosity' was low, therefore both are under selection.

Similar selection pressures influence the shell shape of Nucella lapillus L. (Kitching, Muntz & Ebling, 1964). Nucella from the open coast

have a wider shell aperture than those from a nearby inlet; moreover open coast Nucella show greater powers of adhesion, and less resistance to crab predation.

On boulder shores, the most important selection pressures appear to be crab predation and crushing by boulders and stones (Raffaelli, 1977). Crabs such as Cancer pagurus L., Carcinus maenas L., and Portunus puber L. are generally considered to be important predators of Littorinids (Pettit, 1975). Some of the snails attacked by crabs, or damaged by boulders are able to repair their shells (Raffaelli, 1977). Therefore the proportion of L.rudis with shell injuries in a particular population reflects the intensity of predation by crabs, and crushing by boulders. Raffaelli (1977) found the highest incidence of shell injuries on boulder and stone habitats. However, thickness of shell is not closely correlated with risk of injury. Also, the proportion of shell injuries gives no evidence of predation by birds, who tend to ingest the entire prey (Pettit, 1975). Parasitism is prevalent on boulder shores, and must affect the fitness of L.rudis, as the cercarial infection causes castration (James, 1965; Raffaelli, 1976).

The reproductive strategy of each winkle is an adaptive response to the particular selection pressures of its habitat. The life history tactic which produces the greatest number of offspring will optimise the following: size of offspring, number of offspring, and age at which reproduction occurs. It is generally assumed that there is a cost associated with reproduction; increasing diversion of limited resources to reproduction will lead to decreased survival (e.g. Gadgil & Bossert, 1970; Pianka & Parker, 1975; Horn, in Krebs and Davies, 1978). Evidence for this has been found in rotifers (Snell & King, 1977) and beetles (Murdoch, 1966; see also Stearns, 1976). The optimal reproductive tactic will vary with predictability of the environment, and the difference between adult and juvenile mortality (Hirshfield & Tinkle, 1975; Stearns, 1976).

Field studies to test theoretical predictions in L.rudis are rather few. Faller Fritsch (1977) has shown that winkles in exposed habitats produce large numbers of small embryos per annum, whereas in shelter embryo production

involves fewer numbers, but greater individual size. He suggested that a large number of offspring is favoured in exposure, as recruitment involves colonisation of suitable small crevices. On unstable boulder shores in shelter, juveniles may be particularly susceptible to crushing, burial and desiccation. Hence production of large young is advantageous, (Faller Fritsch, 1977). However, Raffaelli (1976) found no consistent relationship between habitat and embryo size. Berry (1961) investigating reproduction at various shore levels, found that females at higher shore levels had higher average numbers of eggs and embryos in their brood pouches. By transferring winkles from one shore level to another, he showed that females rapidly acquired the characteristic number of embryos of the region to which they were transferred. This result takes no account of embryo size, or reproductive effort involved, but it does suggest that environmental conditions may have a significant proximate effect on winkle reproduction.

In this project, I studied three populations of the winkle L.rudis, each in a different habitat. Atkinson (unpubl. data) had already shown that two of these populations vary markedly in their size structure. I hoped to determine why these three populations are different, by investigating the selection pressures most likely to be important in each habitat.

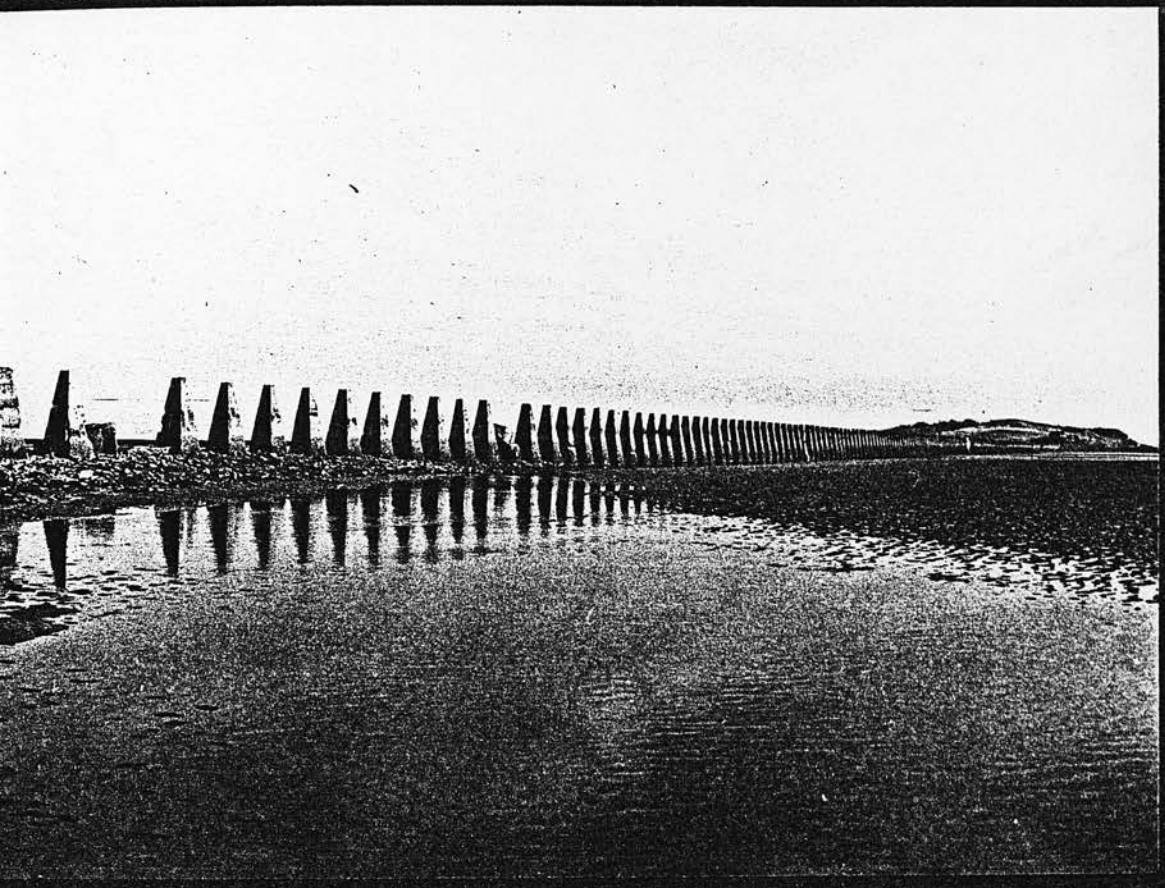


Plate 1: General view of study sites, showing the 'Causeway' piles to the left, and Cramond Island to the right.

STUDY SITES

The three populations studied are found in the intertidal zone at Cramond, which is to the west of Leith, on the Firth of Forth. (plate 1) Two of the winkle populations, 'Island Top' and 'Island Bottom' are on an easterly facing beach on Cramond Island (grid reference: NT 196 783). On Ballantine's (1961) exposure scale, this beach is 'very sheltered' (7); on Lewis's (1964) scale it is 'sheltered' (4) (see fig. 1 and 2). The 'Causeway' population is found among encrusting barnacles on concrete submarine traps which lead out towards the island (grid reference: NT 195 781). Access to the island is possible for 2 hours before and after low tide.

ISLAND TOP

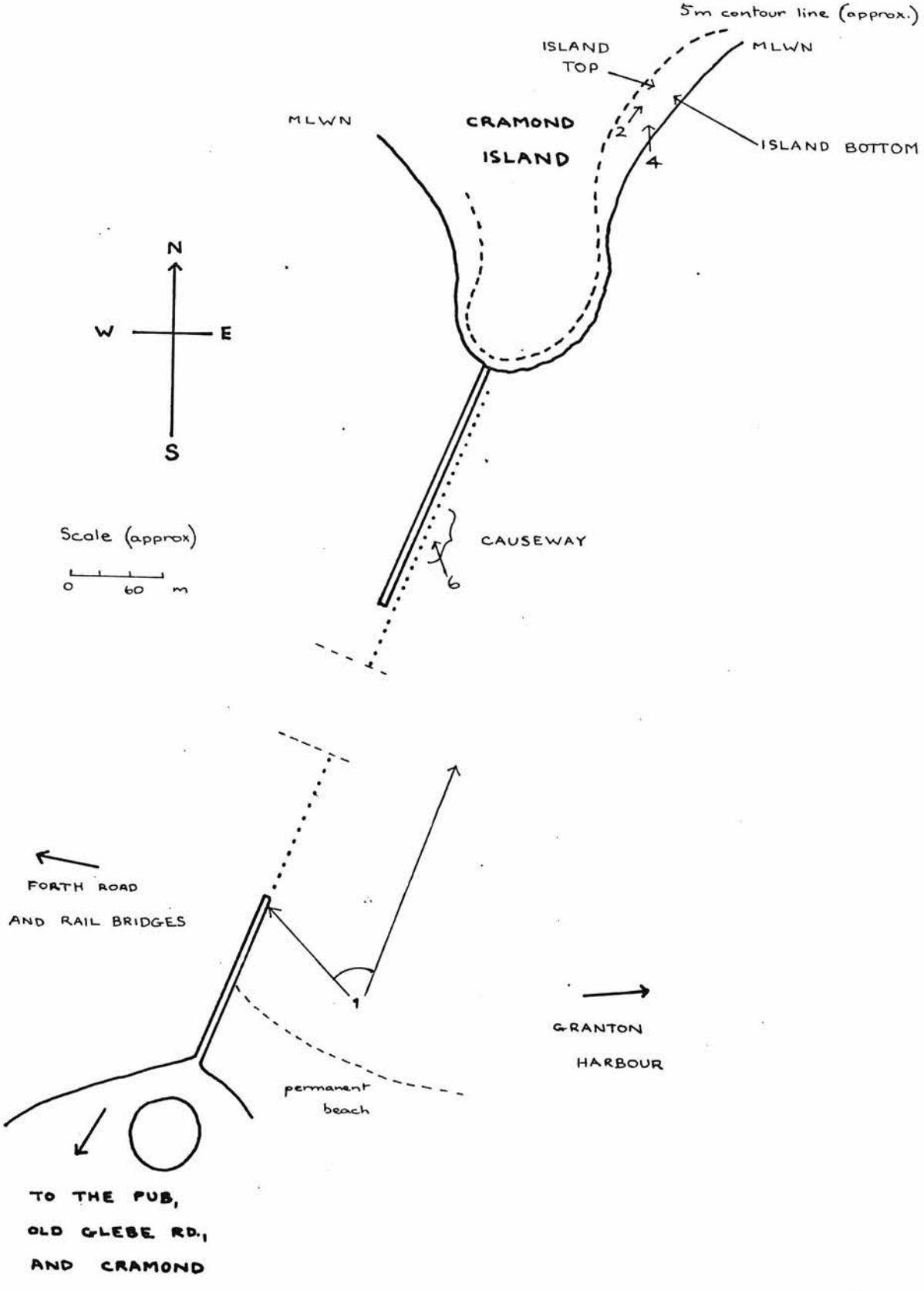
Winkles belonging to this population live on, and under, the large boulders and smaller stones which make up the habitat (see plate 2 and 3). The 'Island Top' site is approximately 4.8 m above Leith datum line, between mean high water neap tides and mean high water spring tides. For 4 to 5 days out of the 14 day tide cycle, these winkles are not covered by high water neap tides.

The site chosen is mainly within the Pelvetia caniculata zone, but extends downshore to where Fucus spiralis and Fucus ceranoides are dominant. Balanus balanoides is present in scattered groups. Other fauna commonly found are Gammarus locusta and Littorina mariae (see Fig.2).

ISLAND BOTTOM

This habitat is much richer in flora and fauna than the 'Island Top' habitat. It is above both the spring and neap mean low water marks, and is covered during every tide. The habitat is made up of large (about 1 m^3) boulders interspersed by stretches of sand (see plate 4) L.rudis are generally found in the crevices among the abundant Mytilus edulis and Balanus balanoides that encrust the boulders (see plate 5). Littorina littorea are more plentiful than L.rudis, and L.obtusata and L.mariae are common. Fronds of Ascophyllum nodosum, and Fucus vesiculosus generally cover parts of the boulders, behind which the winkles can find damper refuges (see fig.2).

Fig. 1. Sketch map of study area. Figures indicate the site and direction of the appropriate plates.



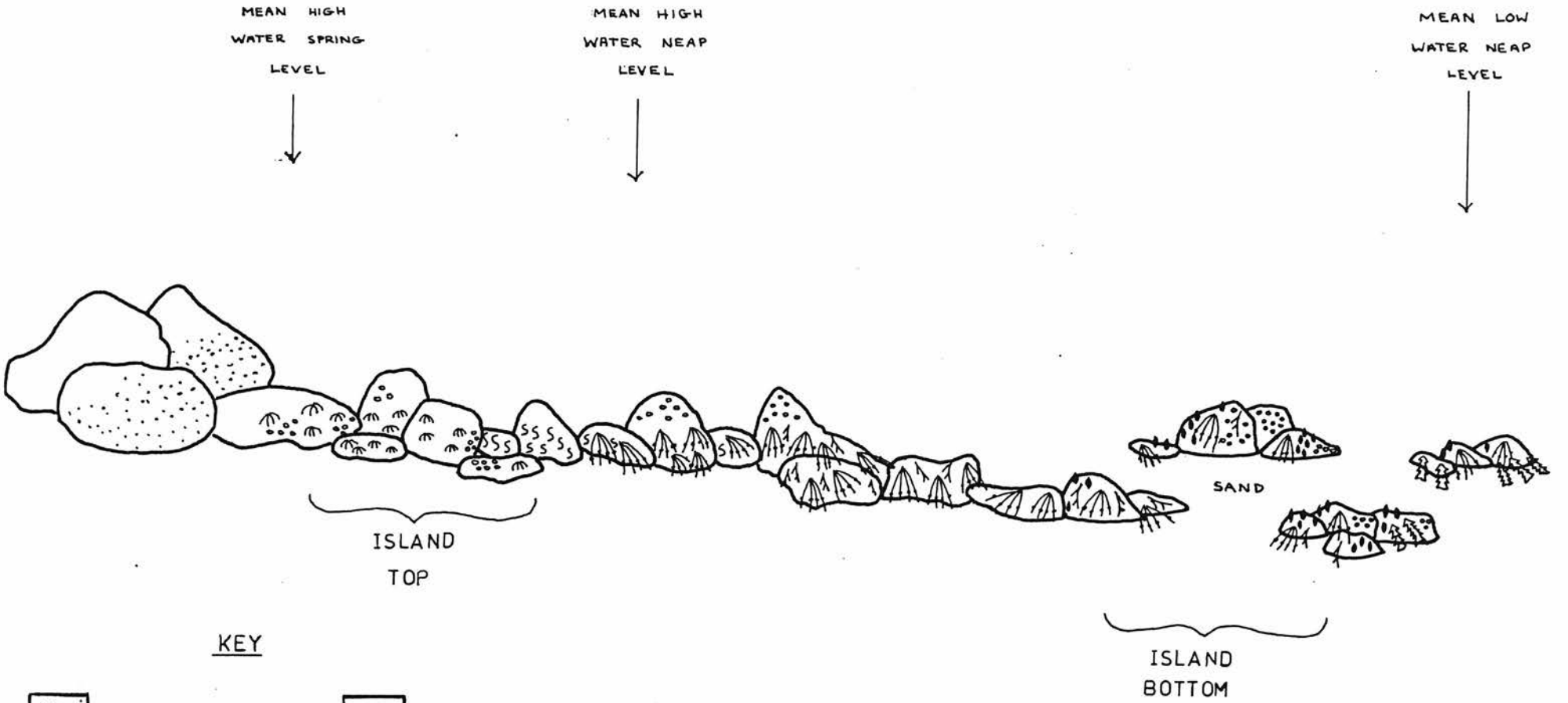


Fig.2 Transect of the beach on which 'Island Top' and 'Bottom' study sites are situated, showing the zonation of dominant flora and fauna.

Plate 2 (above) showing 'Island Top' study site.

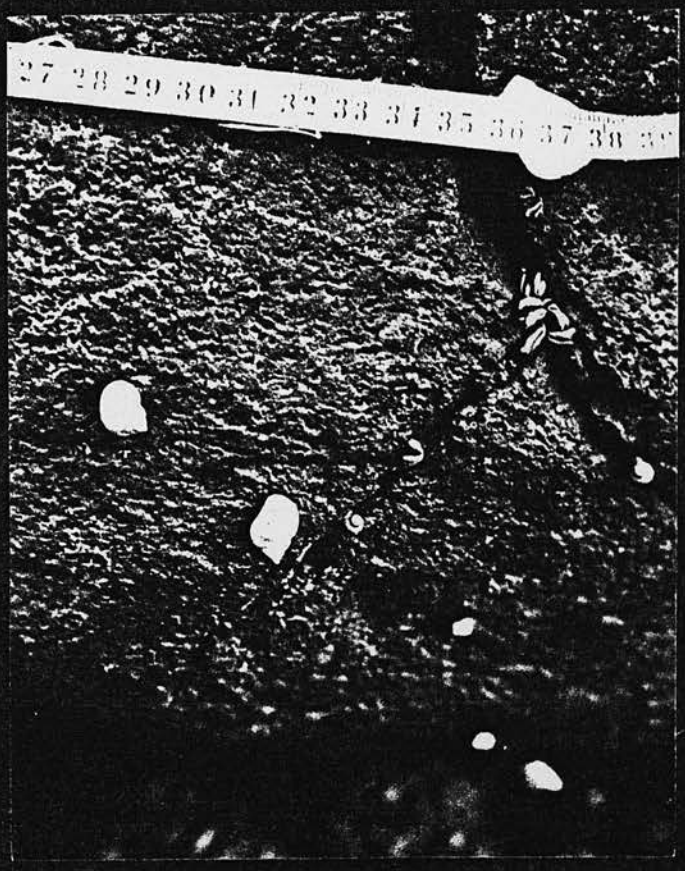


Plate 3 (right) 'Island Top' winkles on the side of a boulder. The scale (cm) is given

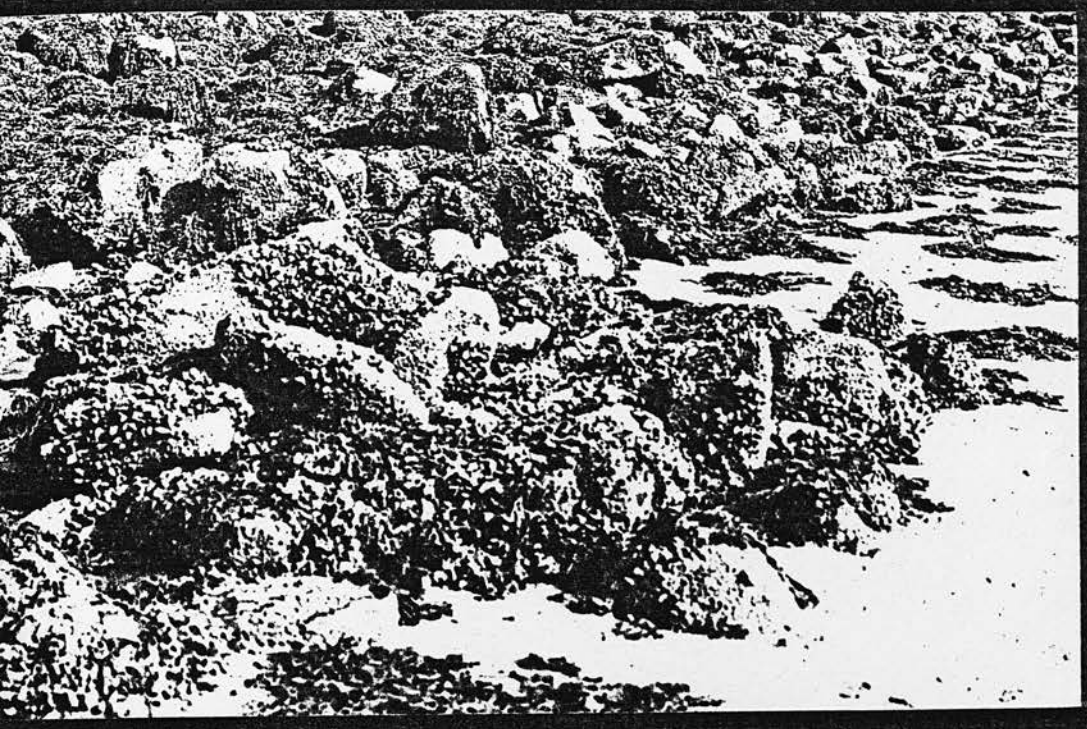


Plate 4 (above) General view of 'Island Bottom' site.

Plate 5 (left) close up of 'Island Bottom' winkles among barnacles on a boulder. Scale (cm) is given.

Beside the walkway to the island is a line of concrete 'piles' or 'pillars' 1.6 m wide at the base and 4 m high, with recesses in the north and south sides (see plates 6 and 7). A short section of this line, 70 m from the island, was chosen for study purposes. The 'Causeway' piles are more exposed than 'Island Top' and 'Bottom' in that they are swept by inflowing and outflowing water during the rising and ebbing tides.

Each pile is encrusted with Balanus balanoides from the base, to 2.4 m above the ground (~~see Fig. 3 and~~ plate 6). This 'barnacle line' marks the mean high water neap mark (Lewis, 1964). L.rudis are found inside dead barnacles, and in crannies between barnacle 'hummocks' (see plate 7) (Lewis, 1964). Mytilus edulis are found in groups up to 0.5 m from the base, and extend further up (0.7 m on the North side, 1.2 m on the South side) inside the recesses. Many Littorina littorea adhere to the surfaces of the mussels, and a few are distributed up to the 'barnacle line'. L.neglecta are common.

When winkles were dissected, to examine aspects of their reproduction, samples were found to be contaminated with about 30% of L.arcana (Hannah-Ford Ellis, 1978; 1979). Unfortunately L.arcana cannot be distinguished from L.rudis by external appearance. Therefore in all experiments where winkles were not dissected, 'Causeway winkles' include both L.rudis and L.arcana.

MATERIALS & METHODS

The project was divided into three separate sections, as follows:

1) Field experiments. Experiments involving some outdoor work, such as marking experiments, sampling etc.
2) Behaviour experiments. Laboratory experiments testing the responses of live winkles under controlled conditions.
3) Reproduction experiments. Measurements of various aspects of life-history tactics.

Each experiment tends to be a complete unit, therefore methods are described elsewhere. Techniques most frequently used are given below:-

Random Sampling

Samples were taken by starting at an arbitrary point on a rock face, or boulder, and collecting all winkles in the path of an increasing spiral, using forceps. In the 'Island Top' habitat, stones and small boulders were overturned, and sampling continued underneath. Usually, 90-110 winkles were collected, as Raffaelli (1976) showed that this number gave stable size distributions.

Markings

'Rowney' acrylic fluorescent waterproof paint was used to mark winkles. If this paint is allowed to dry for 15 minutes after application, it forms a hard-wearing, conspicuous mark, which does not lift or rub off. L.rudis on the shore retained their marks for over 6 weeks.

Measuring

Winkles under 1 cm in shell height (see fig.5) were measured under a 'Kyowa' binocular microscope (x 10 eye piece; x 0.7 to x 4.5 zoom lens) using a measuring graticule. The winkles were held in position by a layer of glass chromatography beads (1.1 or 0.5 mm in diameter) at the bottom of a glass watch glass, filled with sea-water. Larger winkles were measured using 'Camlab' dial calipers. For both large and small winkles, shell measurements were made to the nearest 0.1 of a millimetre. Twenty seven winkles were measured by both calipers and microscope graticule. The results were not statistically different ($t_{27} = 0.250$; $p > 0.8$).

Keeping live collections

L.rudis collected from the shore were kept in plastic boxes (14 x 14 x 20 cm) containing a little sea-water. The boxes had lids to prevent escapes, and were ~~kept~~ maintained at a temperature of 20°C. Winkles were usually kept without food, and used soon after collection. Starved winkles can survive for 40 days (James, 1965; Atkinson, personal communication), therefore the behaviour of winkles kept for a few days without food is unlikely to be affected.

Statistics

The 5% level of significance was used unless stated otherwise.

FIELD EXPERIMENTS

1.MONTHLY SAMPLING

Introduction

The aim of this experiment was to determine the size structure of each population, and to monitor any changes occurring during the 5 month experimental period.

Method

Random samples were taken from each habitat at monthly intervals. The winkles were taken back to the laboratory, and their shell height (see fig.4) measured.

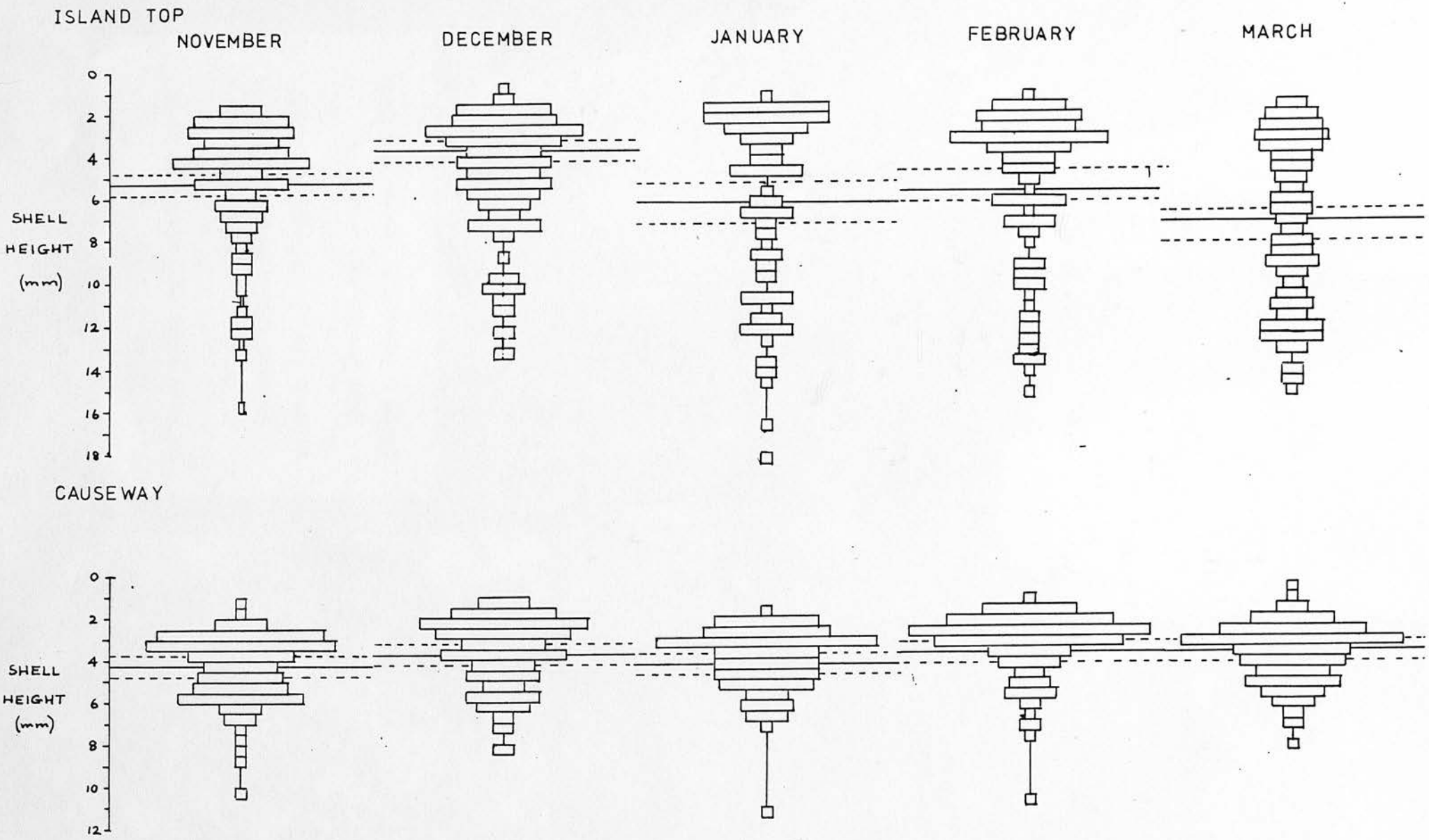
Discussion of Results

The results of this experiment (see Fig.3) must be interpreted rather cautiously, as sampling error is bound to occur. The smallest size classes (< 3 mm) are most likely to be underestimated. However, results do show how different are the size structures of each population. In the 'Causeway' population, few winkles are found over 8 mm. Size frequencies do not change significantly over the 5 months (see Table 1). Such a stable size structure indicates that, at least over the 5 month period studied, the overall selection pressures affecting each winkle size class, are not altered by weather conditions. Size frequencies of the Island Bottom population are more normally distributed than the other two. The smallest size classes in this population are generally found deep down in crevices between mussel shells, so are likely to be

Plate 6 (above) A 'Causeway pile'.
Note recess on south side.

Plate 7 (left) close up of 'pile'
showing many 'Causeway' winkles
in crevices between barnacles.

In both cases the scale (mm or cm)
is given


ISLAND TOP
NOVEMBER
DECEMBER
JANUARY
FEBRUARY
MARCH
SHELL HEIGHT (mm)
0
2
4
6
8
10
12
14
16
18
CAUSEWAY
SHELL HEIGHT (mm)
0
2
4
6
8
10
12

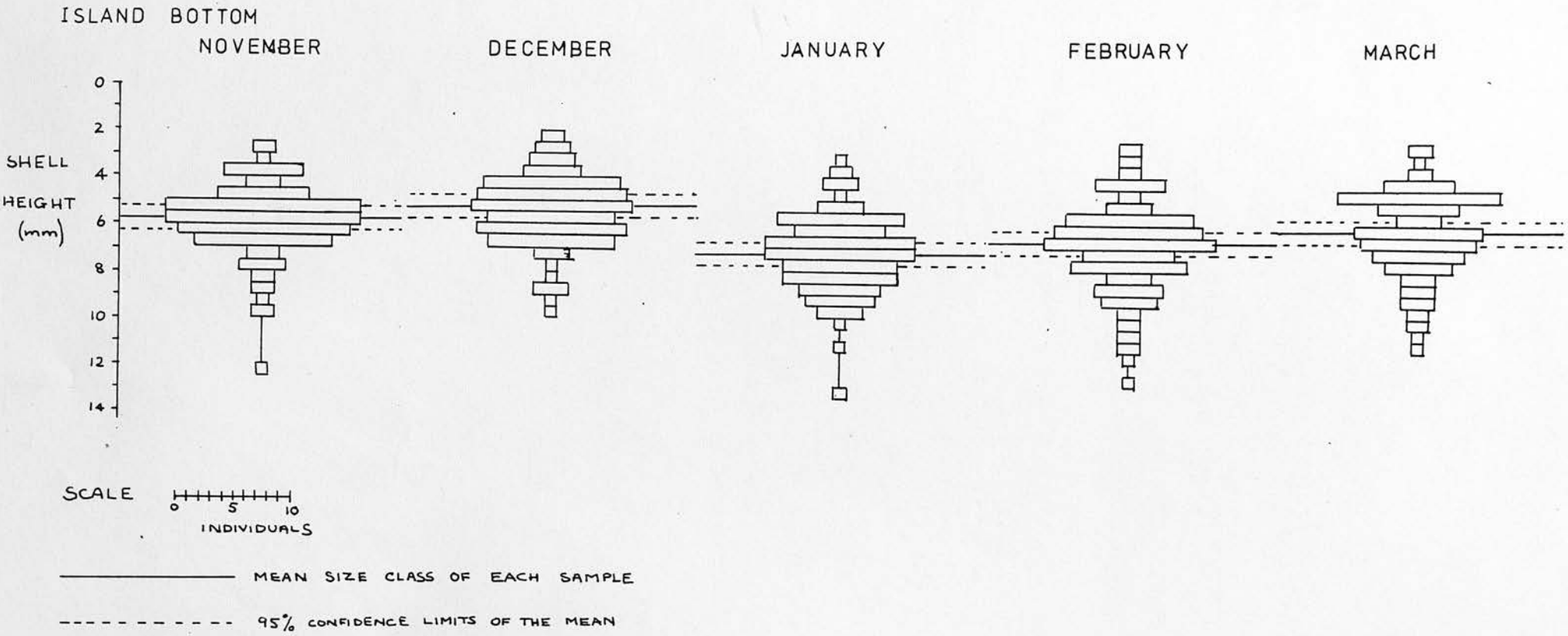


Fig.3 : Shell height distributions of random samples taken at monthly intervals. Each size class frequency is expressed as a percentage, so that comparison is possible.

Table 1

Analysis of data obtained from random monthly samples

ISLAND BOTTOM

Sample date	December 21st	November 24th	March 26th	February 24th	January 26th
Sample size	143	91	93	118	96
Mean shell height	5.36	5.913	6.297	6.885	7.18

$F^{4}_{536} = 21.91 \quad p < 0.01$

ISLAND TOP

Sample date	December 21st	November 24th	February 24th	January 26th	March 26th
Sample size	118	162	105	85	116
Mean shell height	3.880	5.300	5.583	6.272	7.441

$F^{4}_{581} = 14.409 \quad p < 0.01$

CAUSEWAY

Sample date	February 24th	December 21st	March 26th	January 26th	November 24th
Sample size	111	124	105	90	137
Mean shell height	3.660	3.680	3.884	4.070	4.245

$F^{4}_{562} = 1.764 \quad p > 0.10$

Tests used : analysis of variance, and Student-Newman-Keuls test.
Island Top data was transformed to natural logarithms before analysis.
Means not significant at the 95% level are underlined

undersampled. Alternatively, the size distribution may reflect low rate of production of young. Size distributions in successive months are significantly different (see Table 1), but do not appear to change in a predictable pattern. 'Island Bottom' winkles tend to be larger than 'Causeway' winkles but few of them are over 11 mm. Very large winkles (18 mm) are found among the 'Island Top' population. Size distributions are significantly different from each other, and the means show a general upward trend (Table 1). A dramatic change in size frequencies from a population dominated by the smaller sizes,to a population where snails from 2 mm to 13 mm are equally represented, occurs between February and March. In this population, unlike that of the 'Causeway', selection pressures against the smallest size classes appear to increase as a result of changing weather conditions.

2. RELATIONSHIP OF VARIOUS SHELL PARAMETERS

Introduction

In the introduction I discussed why shell shape is related to the degree of exposure. Dislodgement by wave-action must be an important mortality factor for 'Causeway' winkles. The degree of exposure is higher on the 'Causeway' than on the Island, as it is open to winds and waves from all directions. On either side of the piles are sandy flats, unsuitable habitates for winkles. One would expect, therefore, that on the 'Causeway' there would be a high selection pressure for winkles to hang on, since letting go would mean almost certain death. This selection pressure could result in winkles with a larger foot area, and greater foot strength, than those on the island. This experiment was designed to test the hypothesis that shells from an exposed habitat have wider apertures and are more globose, than those from a more sheltered habitat.

Method

Random samples were collected from the 3 habitats. Shell height, shell diameter, mouth height and mouth diameter were measured on each animal (see fig. 4). These measurements were adapted from those of Heller (1975).

Results and discussion

When results for shell diameter, mouth height, and mouth diameter were

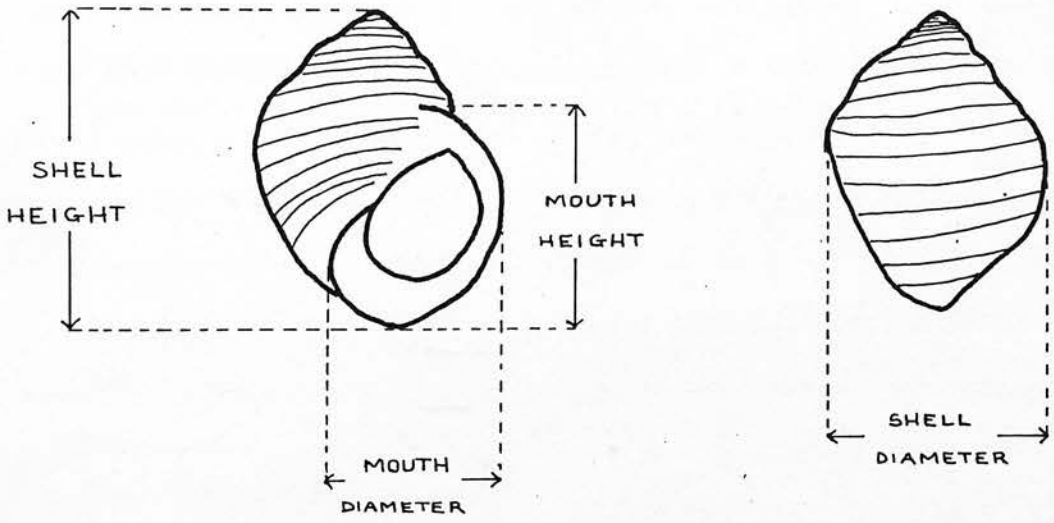


Fig.4 Shell shape measurements taken.

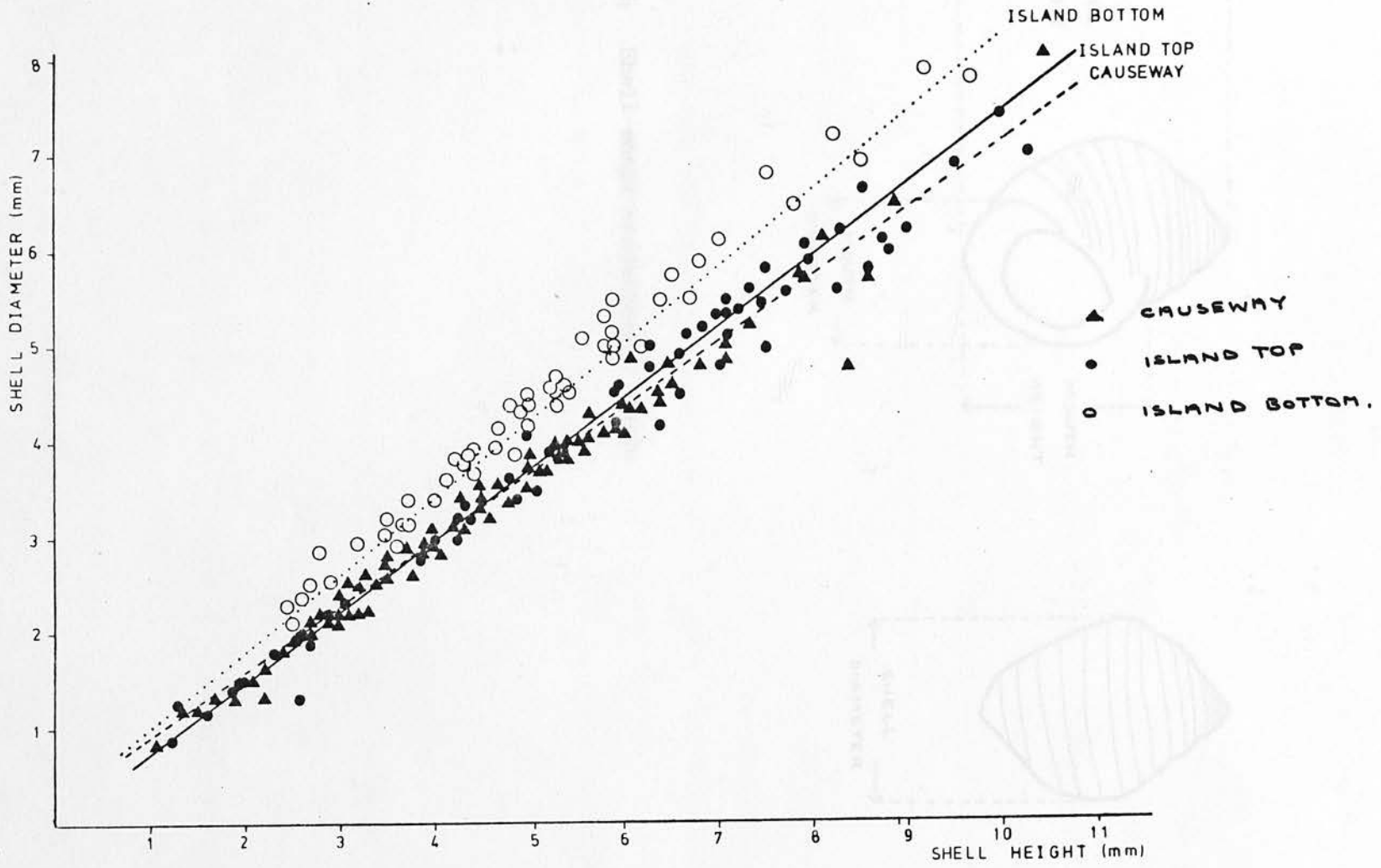


Fig. 5: Shell diameter as a linear function of shell height for the three populations studied.

plotted against shell height, they gave straight lines, regression analyses were carried out on each line. Results are summarized in Table 2. Shell height plotted against mouth height, and against mouth diameter are not significantly different for all three populations. However, shell height versus shell diameter is significantly different for each population. 'Island Bottom' shells are more globose than either 'Island Top' or 'Causeway' shells. 'Causeway' shells are more globose than 'Island Top' shells only up to 4 mm in height (see Fig.5). The predictions of the original hypothesis are not born out.

If exposure can be inferred from shell 'globosity', then the 'Island Bottom' habitat is most exposed. This may be so, if waves crashing onto the beach exert more force than waves in other habitats. However, Heller (1975) did not prove that animals with more globose shells had stronger foot muscles. Therefore, differences in 'globosity' may be adaptive for other purposes.

There are two reasons why mouth width, and mouth diameter are similar for each population. Firstly, the snails may interpret the exposure of each micro-habitat as being similar. Secondly, selection pressures opposing increase in mouth aperture (e.g. desiccation), may prevail, even if exposure is high.

3. FREQUENCY OF SHELL INJURIES

Introduction and Method

Shell injuries may result from crab predation, or from crushing by stones and boulders (Raffaelli, 1977). Carcinus maenus locates the snail by smell (Crothers, 1968) and then systematically breaks away the shell around the body whorl until the soft tissues become accessible. Fifty per cent of attacked winkles are dropped, and escape with a damaged shell, which is later repaired (Raffaelli, 1977). A proportion of shells damaged by boulders will similarly be repaired. Therefore, the frequency of shell injuries in a population indicates the intensity of predation by crabs, and crushing by boulders. The 'Island Top' habitat was expected to have most shell injuries, as it has loose boulders, and is almost certainly visited by crabs during high tide.

Table 2

Table showing relationships of shell diameter (SD), mouth height (MH) and mouth diameter (MD) with shell height (SH).

Population	No.	Equation	95% confidence limits of b	Value of 't'	Degree of significa
Island Bottom	1	SD = 0.800 SH + 0.205	± 0.0277	47.90	p < 0.00
	2	MD = 0.515 SH + 0.427	± 0.0396	25.75	p < 0.00
	3	MH = 0.465 SH + 0.465	± 0.0362	34.06	p < 0.00
Island Top	4	SD = 0.746 SH - 0.0499	± 0.0150	82.16	p < 0.00
	5	MD = 0.510 SH + 0.226	± 0.0110	91.07	p < 0.00
	6	MH = 0.653 SH + 0.0985	± 0.0121	107.20	p < 0.00
Causeway	7	SD = 0.685 SH + 0.218	± 0.0275	41.26	p < 0.00
	8	MD = 0.6012 SH + 0.0469	± 0.117	10.66	p < 0.00
	9	MH = 0.647 SH + 0.0104	± 0.0222	57.56	p < 0.00

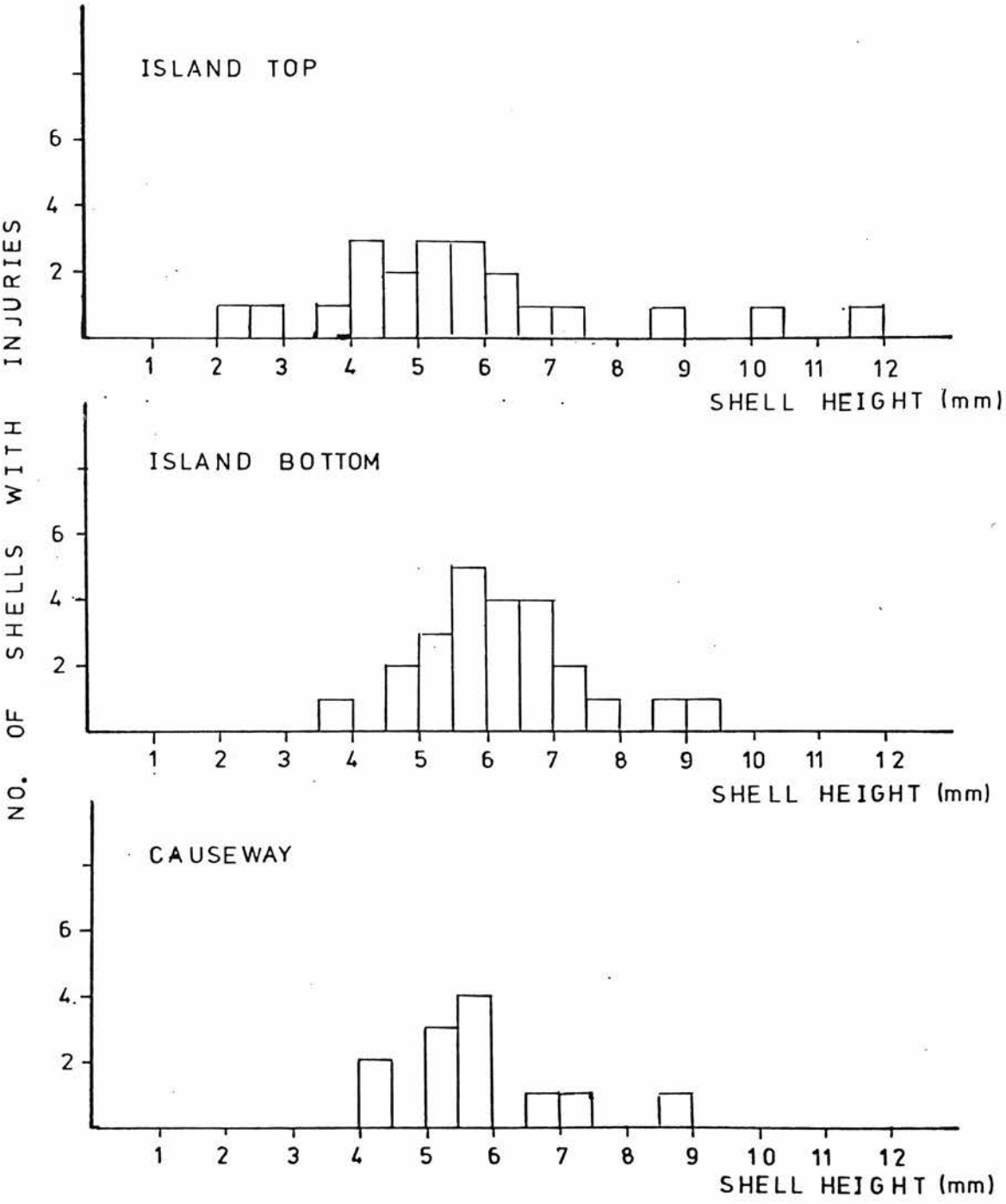
Testing siginificance of comparable equations from each population

Comparing 1, 4 and 7 : confidence units do not overlap, therefore these line are significantly different.

Comparing 2, 5 and 8 : confidence units overlap the means, therefore these are not significantly different.

Comparing 3, 6 and 9: $F^{2}_{384} = 1.622$ $p > 0.10$. n.s

Fig.6 Shell height distributions of shells with injuries.



Percentage of shells injured

Island Top	13%	$\chi^2_2 = 13.28$ $p < 0.005$
Island Bottom	26.5%	
Causeway	8.76%	

A shell injury was defined as a jagged, stepped 'fault', running across the animal's shell. The number of shell injuries was recorded in the preceding experiment. The frequency of shell injuries in each 0.5mm size class is shown as a histogram (Fig.6).

Discussion of results

Results (fig.6) indicate that most shell injuries occur at the 'Island Bottom' habitat. Carcinus maenus, the main predator of winkles, advances up the shore as the tide comes in, and retreats when the tide goes out (Crothers, 1968). The 'Island Bottom' habitat is covered during every tide, therefore crabs will have more opportunity to reach it than the 'Island Top' habitat. Since crushing by boulders in the 'Island Bottom' habitat must be minimal, the proportion of shell injuries appears to reflect only crab predation. The size distribution of shells with injuries, indicate that few shells about 9 mm in height are affected. Most animals over 9 mm may have thick enough shells to resist predation or crushing.

If there is a constant chance of injury throughout at least part of a winkle's life, a cumulative or skewed distribution of shell injuries would be expected. That the curves shown (fig. 6) are not skewed indicates that injured winkles suffer a lower survival rate than uninjured individuals.

It is surprising that shell injuries occur among the 'Causeway' population. Possibly, they are caused by another environmental factor, such as pounding by waves.

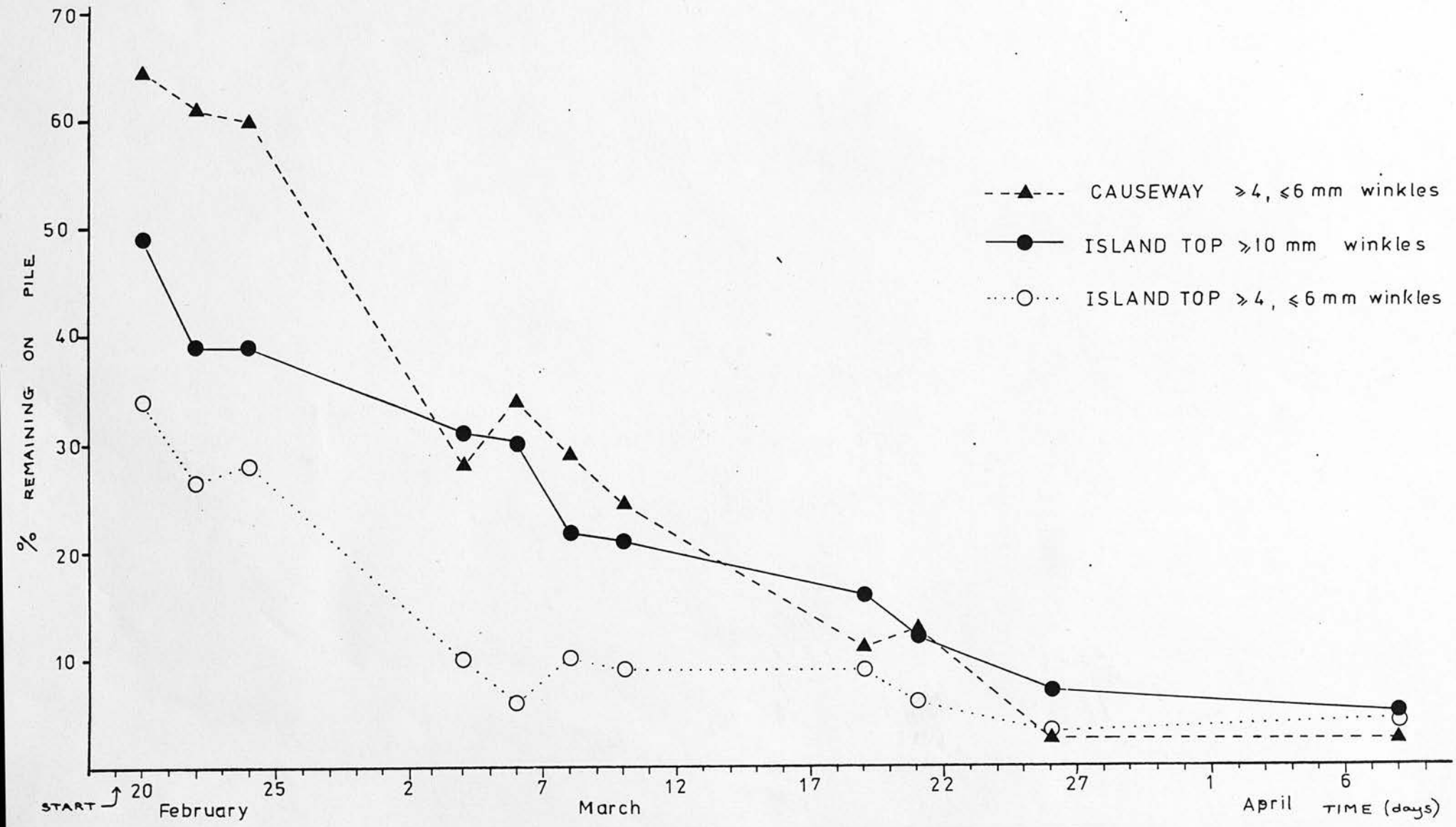
The agents that cause shell injuries require further investigation before the suggestions made can be verified.

4. SURVIVAL OF LARGE WINKLES ON THE CAUSEWAY PILES

Introduction

In the introduction, I discussed how availability of suitable crevices affects winkle population dynamics. Because winkles wedge themselves in crevices to prevent dislodgement, the maximum size that can be attained by each winkle is determined by the size of available crevices (Emson and Faller Fritsch, 1976; Raffaelli and Hughes, 1978). On the 'Causeway' piles, only crevices between barnacles are available. Therefore, when winkles outgrow

Fig.7 Graph showing fall-off rate of various groups of winkles transferred to a 'Causeway' pile. The frequencies at the start of the experiment (ie. 100%) are not shown.



these crevices, they will be washed off. This theory could explain why there are very few large (> 8 mm) winkles in the 'Causeway' population. An experiment was designed to test the above hypothesis.

Method

A 'feasibility study' was done between November and February to try out techniques. Between the end of February and April, a more detailed experiment was carried out.

Samples of winkles were collected from the 'Island Top' and 'Causeway' habitats, and taken back to the lab in polythene bags. The 'Island Top' collection was separated into two size classes; $\geqslant 4$ mm, $\leqslant 6$ mm and $\geqslant 10$ mm. Among the 'Causeway' control winkles only $\geqslant 4$ mm, $\leqslant 6$ mm winkles were used. Each class contained 70 to 100 winkles. The three groups were marked with different colours of acrylic paint, and placed in a tank overnight. On the following day, the marked winkles were taken to the 'Causeway' habitat, divided into two replicate samples, and pressed into crevices on the east side of two of the piles. Numbers of marked winkles remaining on the piles were recorded the next day, and at 2 day intervals, during periods when it was possible to walk out to the 'Causeway' habitat in daylight. Little difference was found between replicates, so the results were pooled. For each size class, the numbers remaining on the pile after each count was expressed as the percentage of those originally put on (see fig. 7).

Kitching et al. (1964) have tested adhesion of Nucella lapillus to an exposed rock surface using similar methods.

Discussion of results

This experiment is rather biassed in favour of large winkles, as these are easier to see. At some points, (fig. 7), the number of smaller winkles on the pile increases. There are two possible reasons for these increases. Firstly, winkles that have been washed off the pile could climb back. This behaviour is possible, as it was observed for one specially marked large winkle. The second explanation is that on one day some winkles crawl deep inside barnacles, so are missed, but on the next day they climb out to where they are easily seen.

Table 3

Weather conditions during desiccation experiment.

	Air temperature °C	Wind Direction (degrees)	Wind Speed (knots)
9th March (experiment 1)	7	255 (West-South West)	14
2nd April (experiment 2)	8	270 (West)	16

Throughout most of the experiment, small 'Causeway' winkles stay on better than small 'Island Top' winkles. 'Causeway' winkles must have some behavioral or physiological adaptation that 'Island Top' winkles do not have. Large 'Island Top' winkles hang on almost as well as the small 'Causeway' group, despite having few suitable crevices as refuges. The hypothesis outlined in the introduction is not upheld.

A more probable hypothesis is that mortality due to wave dislodgement is high, irrespective of size. The longer each winkle stays on the pile, the more likely it is to be washed off. Therefore few winkles will have a chance to reach a large size.

5. EFFECT OF DESICCATION

Introduction

Towards the end of the study, it was observed that on dry, sunny days, 'Island Top' winkles are only found under stones and overhangs, and not on the faces of boulders, as on damp days. The 'Causeway' piles appear to dry out, but here the winkles have no damp refuges to retreat to. Desiccation is therefore a possible important selection pressure.

This experiment was designed to test the hypothesis that the 'Causeway' habitat is dryer than the 'Island Top' habitat. A further aim was to detect differences in desiccation on each side of a pile, and if differences occur, to investigate the effect on winkle size frequencies, and barnacle heights. The experiment was divided into 3 parts:

(a) Measurement of desiccation

(b) Effect of desiccation on size frequencies of winkles from each side of a 'Causeway' pile.

(c) Effect of desiccation on barnacle height

General method

Both parts (a) and (b) were carried out on 9th March 1980 (Experiment 1) and 2nd April 1980 (Experiment 2). One particular pile (pile 7) was used for all three parts. Sunny, windy days were chosen as selection pressures resulting from desiccation are then most likely to have an important effect. Weather conditions on the day of each study were obtained by 'phoning Turnhouse airport (031 339 7777) (table 3).

5a. Measurement of desiccation

Method

Rate of evaporation from a wetted filter paper was used to estimate rate of evaporation from the rock or barnacle surface. Each filter paper was held in a plastic petri-dish.

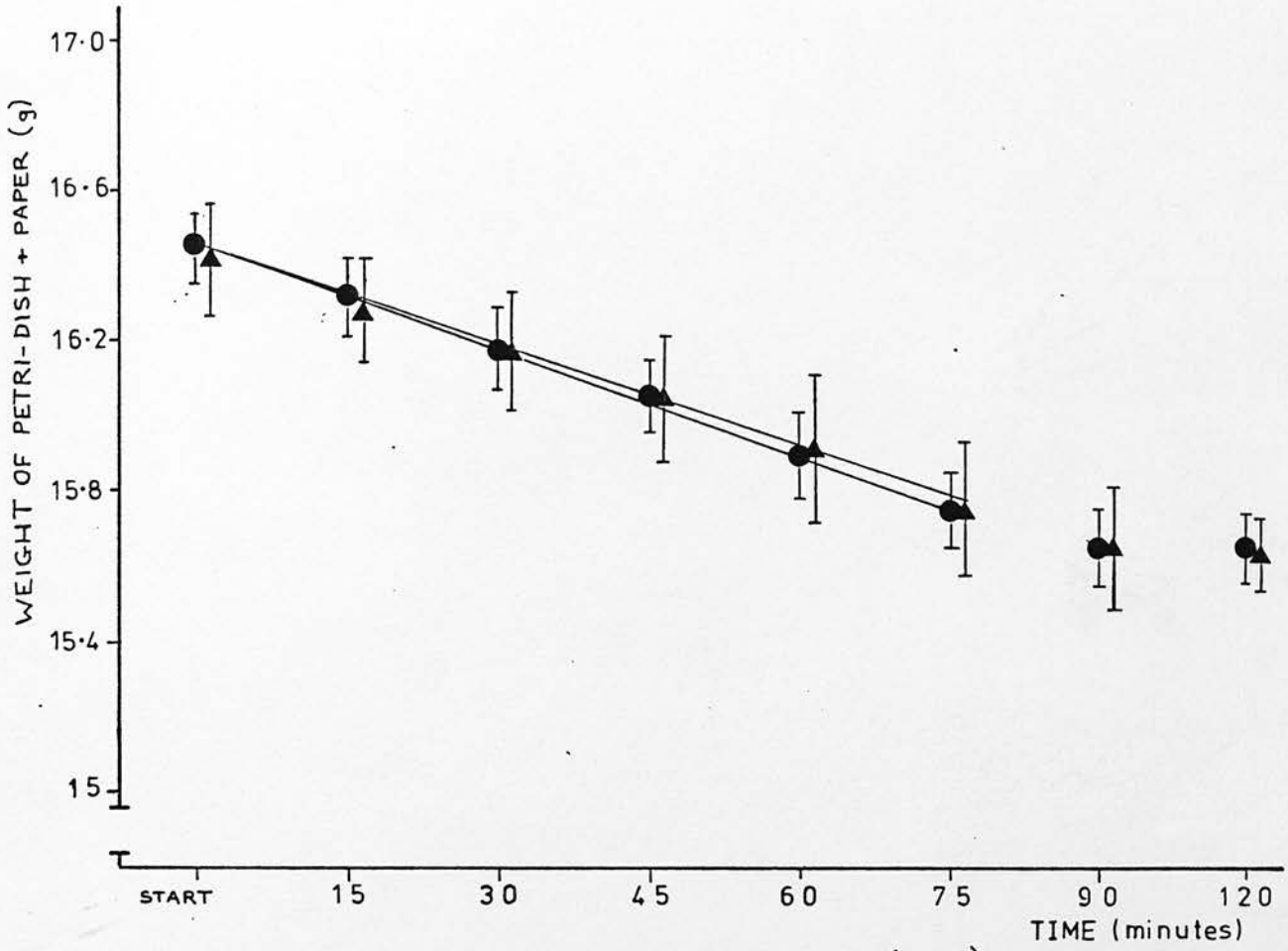
Firstly, the 'drying curve' for a piece of filter paper was required. Two groups of 4 replicate petri-dishes were used. These petri-dishes were cleaned, dried and numbered. A 7.0 cm 'Whatman' filter paper was placed in each. 0.8ml tap water was dispensed onto each filter paper from a burette (0.8 ml is the maximum amount required to saturate a filter paper). Individual petri-dishes plus lids were weighed to the nearest 0.01 g on a Oertling (21 TD) balance. One group of petri-dishes without lids was left in the laboratory ($\sim 20^{\circ}C$): the other group was placed in a constant temperature room ($20^{\circ}C$) which was well ventilated. Petri-dishes, plus lids, were reweighed every 15 minutes. The resulting curve is shown in fig. 8.

Desiccation in the 'Causeway' and 'Island Top' habitats was estimated using weighed petri-dishes prepared in exactly the same way. The prepared petri-dishes were taken out to Cramond. One group of four were left with their lids on, as a control. Petri-dishes without lids were stuck onto each face and recess of pile 7 with 'Bluetack'. 'Island Top' sites were tested by placing uncovered petri-dishes where winkles were found, i.e. under overhangs and stones. In each case, 4 replicate dishes were used for each site. After 1 hour (Experiment 1) or 3/4 hour (Experiment 2) the petri-dish lids were replaced, and the dishes taken back to the lab and reweighed. Differences in weight were calculated, and analysed by a one way analysis of variance and a Student-Newman-Keuls test (Sokal and Rohlf, 1969).

Discussion of results

The drying curve for a 7.0 cm filter paper is linear except for the last two readings. Results of the two groups at the same temperature, but in different places, agree closely. Therefore, comparison between 'Causeway' and 'Island' desiccation measurements was felt to be fully justified, provided that the linear part of the drying curve was used. The period that filter papers

Fig.8 'Drying curve' of a 7.0 cm filter paper.



● FILTER PAPER DRIED IN THE LABORATORY (~20°c)

▲ FILTER PAPER DRIED IN A CONSTANT TEMPERATURE ROOM (20°c)
(points displaced to right for clarity.)

Regression equations (excluding last two points)

● $Y = 16.468 - 0.0094X$ (± 0.00636) $t_5 = 40.94$; $p < 0.001$

▲ $Y = 16.448 - 0.0090X$ (± 0.0127) $t_5 = 23.943$; $p < 0.001$

were left to dry outdoors was arbitrary. In the first experiment, 1 hour was too long, as some papers blew away, resulting in missing data.

In both experiments, results (see Table 4) agreed with expectations. Control plates lost the least water, 'Island Top' plates a little more, and 'Causeway' plates the most. Therefore 'Causeway' winkles have to endure more severe desiccation than those from the Island. Within the 'Causeway' habitat, the driest faces tend to those facing the sun or wind, while the wettest places tend to be the recesses. Differences between the two experiments result from particular weather conditions. During Experiment 1, the wind blew straight into the South recess, resulting in more water loss than Experiment 2. The dryness of the eastern face, in Experiment 2, is due to the morning sun shining directly upon it.

5b. Effect of desiccation on size frequencies of winkles from each side of a 'Causeway' pile.

Introduction

In Experiment 5a, each side of a 'Causeway' pile was shown to have a different rate of desiccation. Desiccation tends to affect smaller winkles more than larger ones (Raffaelli, 1976.) If winkles are relatively mobile, they may tend to move to the wettest places they can find during a period of desiccation. If they are only slightly mobile, differential mortality will take place on each face; on dry places, a high proportion of small winkles will die. The aim of this experiment was to test whether the amount of desiccation on each side of the pile affects the size frequencies found; and if it does, in what way are size frequencies affected.

Method

Random samples were taken from each side of the pile, and from North and South recesses. The snails were taken back to the lab, and their shell heights measured. Results were analysed by a one-way analysis of variance, and a Studen Newman-Keuls test. For each face, (or recess) results obtained for Experiment 1 were tested against those of Experiment 2, using a t-test. Only the two samples from the South recess were found to be significantly different. The

Table 4 (a) Measurement of desiccation

Experiment 1

Sample	Control	Island Top	Island Top	Island Top	North recess	North face	East face	South recess	West face	South face
Number of replicates	4	4	4	4	4	4	4	4	2	0
Mean amount of water lost (g)	0.0525	0.147	0.157	0.212	0.330	0.450	0.580	0.597	0.70	
± 95% confidence limits	0.0475	0.0614	0.0739	0.0845	0.0468	0.0998	0.0344	0.1501	5.82	

From analysis of variance between samples: $F^{8}_{25} = 235.037$: $p < 0.01$

Experiment 2

Sample	Control	Island Top	Island Top	Island Top	Island Top	South recess	North recess	West face	North face	South face	East face
Number of replicates	4	4	4	4	4	3	4	4	4	3	3
Mean amount of water lost (g)	0.0250	0.0750	0.080	0.0925	0.1425	0.257	0.260	0.285	0.340	0.450	0.513
± 95% confidence limits	0.0506	0.0379	0.0431	0.0438	0.0301	0.0759	0.0623	0.0205	0.120	0.262	0.317

From analysis of variance between samples: $F^{10}_{30} = 45.22$: $p < 0.01$

probability that samples are found significantly different due to chance alone is high (0.26). Therefore, I felt I was justified to pool the results (table 5).

Discussion of results

General trends shown in the results (table 5) are that East face, South face and North face tend to have populations of small winkles; South recess and North recess have large winkles, while West face falls in-between. As results on days with different weather conditions can be pooled, winkles do not move to suit slight differences in dryness.

5c. Effect of desiccation on barnacle height

On exposed shores, where much wave splash occurs, barnacles are found higher on the shore than in sheltered situations. Shaded positions are preferred by Balanus (Lewis, 1964). On the 'Causeway' piles, barnacles are so abundant that they grow on top of each other. On favourable sides of the pile (i.e. shaded and damp places), I expected the average height of barnacles to be higher than on less favourable sides.

Height of barnacles is likely to affect the distribution of winkles. Where barnacles are high, the crevices between them and among dead barnacles will be large, forming suitable refuge for the larger winkles. Also, the large crevices will trap moisture, providing protection against desiccation. Where barnacles are low, crevices between them will be small, and will dry out quickly. The aim of this experiment was to test whether barnacle height differs on each side of the pile; and if it does, to attempt to correlate the results with 5a or 5b.

Method

The 'Camlab' calipers used have a wire rod which projects from the handle end, when the caliper jaws are opened. The amount that the wire projects is equal in length to the measurement recorded on the dial. Barnacle heights were measured by inserting the projecting wire rod into a dead barnacle, so that the end touched the concrete base. The calipers were then adjusted, so that the end of the plastic handle touched the opening in the barnacle. The measurement wa read off the dial to the nearest 0.1 mm.

Table 5

(b) Analysis of shell heights of winkles taken from each side of a 'Causeway' pile (pooled results)

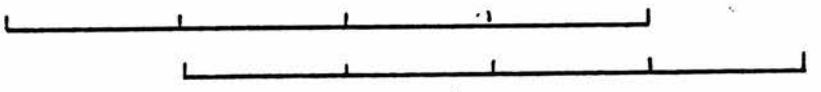
Sample	South face	East face	North face	West face	North recess	South recess
Number in sample	169	190	226	174	190	180
Mean shell height (mm)	3.693	3.742	3.924	4.292	4.661	4.714
± 95% confidence limits	0.209	0.228	0.197	0.409	0.208	0.220

From analysis of variance between samples $F^{5}_{1131} = 12.43$; $p < 0.01$

Table 6

(c) Analysis of barnacle heights on each side of a 'Causeway' pile

Sample	South face	East face	South recess	North recess	West face	North face
Number of measurements	26	26	26	26	26	26
Mean barnacle height (mm)	8.842	9.896	9.919	10.108	10.365	11.446
± 95% confidence limits	0.723	1.115	1.156	1.140	1.101	1.034



From analysis of variance between samples $F^{5}_{150} = 2.636$; $p < 0.05$

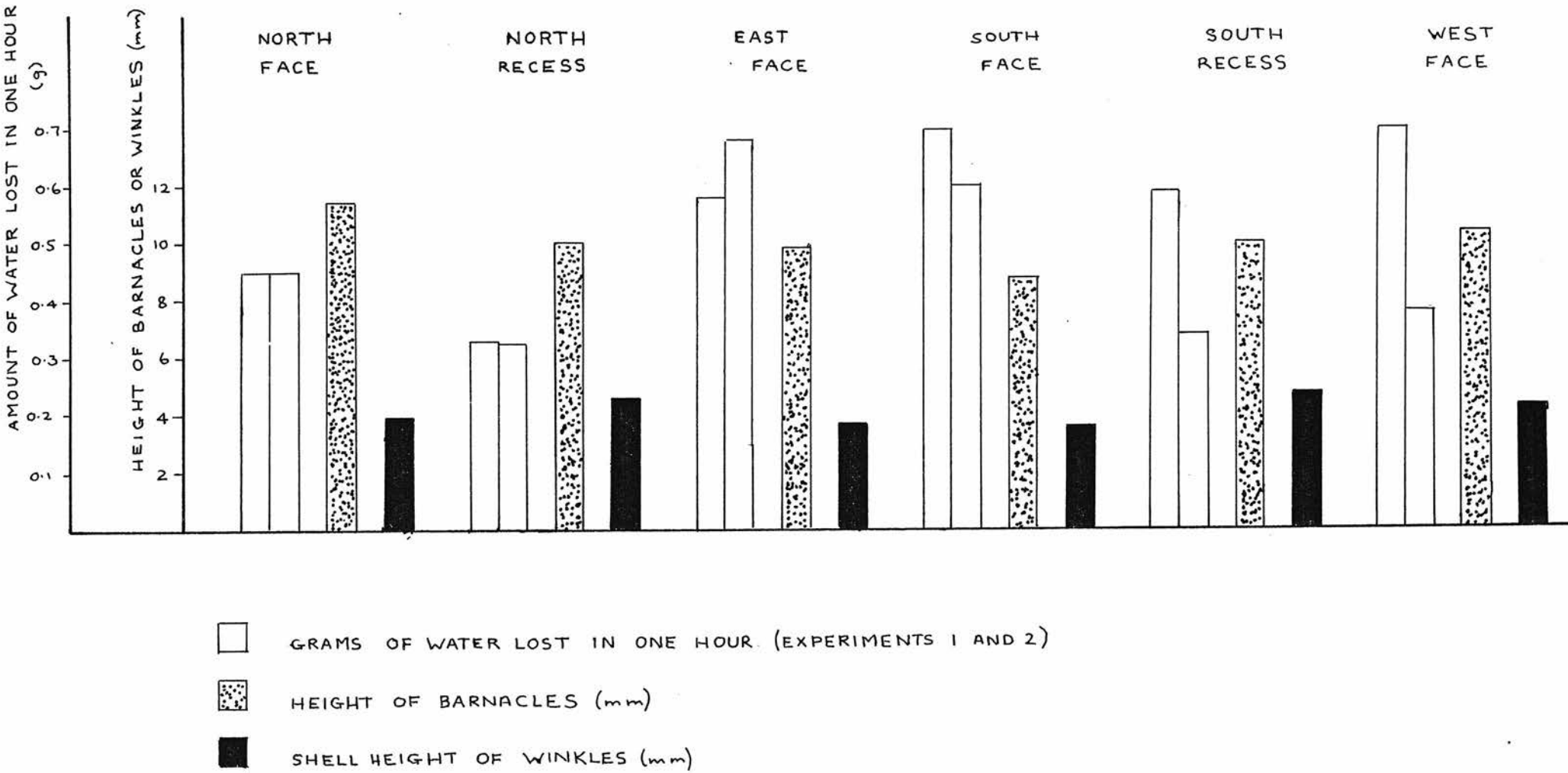
Table 7

Spearman Rank correlations calculated between shell height, barnacle height and desiccation on each side of a 'Causeway' pile

Groups Tested		Spearman Rank Correlation Coefficient	Level of Significance
Shell height	Desiccation 1	- 0.371	ns
Shell height	Desiccation 2	- 0.943	p = 0.01
Shell height	Barnacle height	0.425	ns
Barnacle height	Desiccation 1	- 0.486	ns
Barnacle height	Desiccation 2	- 0.371	ns
Shell height	Desiccation 1 & 2	- 0.885	p < 0.05
Barnacle height	Desiccation 1 & 2	- 0.543	ns

Desiccation: - wet ⟶ dry
ranked as 1 ⟶ 6
Shell height: small ⟶ large
ranked as 1 ⟶ 6
Barnacle height: low ⟶ high
ranked as 1 ⟶ 6

Fig.9 Summary of data abstracted in Experiment 5, showing the relationship between desiccation, barnacle height and snail shell height.



A 130 cm long measuring tape was attached vertically to one face of pile 7 with "Bluetack". The top of the tape was 210 cm from the ground. Measurements of barnacle height were made every 10 cm, using a suitable dead barnacle nearest to the tape. 13 measurements were taken for each tape; the tape was then moved along and replicate measurements made. This process was repeated on each side of the pile, and in the two recesses. The results were analysed in a similar way to that of Experiment 5a and 5b (table 6).

Conclusions

Results (table 6) show that North face barnacles are significantly higher than South face barnacles. This fits the expectation that sunny sites are less favourable than shaded positions. Barnacle heights on other faces are not significantly different from one another.

Analysis of data

Any correlations between shell height, barnacle height and desiccation were detected using the Spearman Rank correlation test (Siegel, 1956). Means obtained from experiments 5a, b and c were ranked as shown in Table 7, and correlation coefficients calculated between each pair. Shell heights and barnacle heights were correlated against results from both desiccation experiments and against combined results. To obtain a combined result the desiccation ranks were averaged, and the averaged results ranked again. This method prevents one set of means from biasing the combined result.

General results and conclusions

Figure 9 summarises the data from Experiment 5. Significant results (Table 7) have a negative correlation coefficient, showing that large winkles tend to live in wet places; and small winkles in dryer places. Barnacle height was neither correlated with shell height nor desiccation. This experiment appears to show that winkle survival is more dependant on dampness of the substrate than on size of crevices. In the introduction to 5b I suggested that, if winkle mobility is low, then higher numbers of small winkles will be killed on the dryer faces. However, winkles found on dry faces are small, rather than large. Possibly, winkles that find themselves in wetter places are able to survive for a long time, and so grow to a large size. Data on winkle mobility is needed to verify this hypothesis. Also, an

experiment proving lower survival of a small winkle under dry conditions is required, as this so far as I know, has not already been done. The dryer nature of the 'Causeway' habitat suggests that 'Causeway' winkles may be better adapted to dry conditions than 'Island Top' winkles. Experiments on survival, and behaviour on desiccation are carried out in a subsequent section.

BEHAVIOUR EXPERIMENTS

These experiments were designed to test the responses of live winkles to simulated aspects of the natural environment. By studying these responses, I hoped to be able to explain more fully the results obtained in the field experiments.

6. 'UPWARD CLIMBING' EXPERIMENT

Introduction

Experiment 4 showed that among winkles of size classes $\geq 4, \leq 6$ mm, 'Causeway' winkles disappeared from the pile at a slower rate than 'Island Top' winkles. This, and the next experiment (Experiment 7) were attempts to find adaptive behaviour differences between winkles from the two habitats. When live winkles were brought into the lab, and were put into boxes containing sea-water, 'Causeway' winkles appeared to climb up the sides of the box faster than 'Island Top' winkles. In the wild, this behaviour could be adaptive, if, for example, 'Causeway' winkles tended to climb up out of reach of breaking waves, which threatened to dislodge them, or if they could climb back onto the 'piles' after being washed off. Tests were performed using 3 surfaces; glass, plastic, and polystyrene.

Method

(a) Glass Surface

Winkles were grouped into 6 size classes (> 4 mm ≤ 5 mm, > 5 mm ≤ 6 mm.... .... > 9 mm ≤ 10 mm), with 4 'Causeway' winkles and 4 'Island Top' winkles in each class. 48 'Samco' flat-bottomed glass tubes (75 x 25 mm) were prepared by pouring equal amounts (~ 2 ml) of sea water into each. Individual winkles were placed in each tube. After 25 minutes (i.e. average time for the first winkle to reach the top of the tube) the height each winkle had climbed was recorded. Heights were measured with a ruler, from the base of the tube

to the lowest part of the foot. Results were analysed by transforming data x to $\log_e (x + 1)$ and using a two-way analysis of variance.

(b) Plastic and polystyrene surfaces

Tests using these two surfaces were performed simultaneously. Four (10 x 10 x 10 cm) plastic boxes with lids were used. Two of the boxes were lined with polystyrene ceiling tiles, which were cut down to size using a hot knife. To make sure that the two sets of boxes had the same light conditions, the two remaining boxes were covered, on the outside, with aluminium foil, so that no light could penetrate the walls. A little sea-water was placed in each box. 'Causeway' and 'Island Top' winkles were divided into small ($> 4, \leq 6$ mm) medium ($> 6, \leq 8$ mm), and large ($> 8, \leq 11$ mm) categories. Approximately 20 small 'Causeway' winkles and 20 small 'Island Top' winkles were placed in each box. Boxes, complete with lids, were left for two hours under overhead lighting. (Two hours is the time required for an appreciable number to climb up the walls). After this period, numbers of 'Causeway' and 'Island Top' winkles on the walls, floor and lid were scored. The height that those winkles on the walls had climbed was measured with a ruler, and noted. Winkles were transferred from one type of box to the other, and the experiment repeated. Other size classes were treated similarly. Results were analysed by χ^2 tests.

Results

(a) Glass surface

'Causeway' winkles do tend to climb out of water faster than 'Island Top' winkles, but results are not significantly different ($F^1_{41} = 3.806$; $0.1 > p > 0.05$ Size does not determine the speed of this reaction ($F^5_{41} = 0.633$; $p > 0.10$). For two way analysis of variance table, see appendix A.

(b) Plastic and polystyrene surfaces

Tables 8 and 9 show a difference in behaviour between size classes. Among the smallest sizes 'Causeway' winkles tend to climb up more readily than 'Island Top' winkles; the reverse is true for the medium size class ($> 6, \leq 8$ mm). However, χ^2 values for the second size class are only marginally significant. There appears to be no difference in the behaviour tested between large winkles. All but one of the t-tests calculated between heights climbed by 'Causeway' and

Table 8

Results of 'upward climbing' experiment.

Polystyrene surface

Size Class (mm)	Replicate	Value of χ^2	Significance Level	
> 4, ≤ 6	a	0.01669	0.9 > p > 0.750 ns	
	b	1.901	0.25 > p > 0.1 ns	
	c	6.690	0.01 > p > 0.005 sig	more 'Causeway' climb
	d	6.300	0.25 > p > 0.01 sig	more 'Causeway' climb
	total	10.327	0.005 > p > 0.001 sig	more 'Causeway' climb
> 6 ≤ 8	a	0	p > 0.995 ns	
	b	2.63	0.25 > p > 0.1 ns	
	c	10.76	0.001 > p > 0.005 sig	more 'Island Top' climb
	d	1.38	0.25 > p > 0.10 ns	
	total	7.60	0.05 > p > 0.01 sig	more 'Island Top' climb
> 8 ≤ 11	a	5.628	0.17 > p > 0.05 ns	
	b	0	p > 0.995 ns	
	c	0.128	0.75 > p > 0.5 ns	
	d	0.377	0.75 > p > 0.5 ns	
	total	0.944	0.500 > p > 0.25 ns	

Table 9

Results of 'upward climbing' experiment

Plastic surface

Size class (mm)	Replicate	Value of χ^2	Significance Level		
$>4 \leq 6$	a	5.579	$0.1 > p > 0.05$	ns	
	b	3.111	$0.25 > p > 0.1$	ns	
	c	0.716	$0.750 > p > 0.500$	ns	
	d	1.701	$0.25 > p > 0.1010$	ns	
	total	7.91	$0.05 > p > 0.01$	sig	more 'Causeway' climb
$>6 \leq 8$	a	0	$p > 0.995$	ns	
	b	0.0160	$0.900 > p > 0.750$	ns	
	c	12.44	$p < 0.001$	sig	more 'Island Top' climb
	d	0.0107	$0.95 > p > 0.90$	ns	
	total	8.188	$0.05 > p > 0.001$	sig	more 'Island Top' climb
$>8 \leq 11$	a	0.209	$0.75 > p > 0.50$	ns	
	b	0.370	$0.75 > p > 0.50$	ns	
	c	0.386	$0.75 > p > 0.50$	ns	
	d	0.190	$0.75 > p > 0.50$	ns	
	total	0.116	$0.75 > p > 0.50$	ns	

Table 10

Comparisons of heights climbed by 'Causeway' and 'Island Top' winkles on plastic and polystyrene surfaces

Surface	Size Class (mm)	Mean height climbed (cm) Causeway	Island Top	Values of 't'	Level of Significance	
Polystyrene	$> 4 \leq 6$	1.695	2.062	0.505	$0.5 > p > 0.25$	ns
	$> 6 \leq 8$	1.106	2.07	1.954	$0.1 > p > 0.05$	ns
	$> 8 \leq 11$	3.653	2.800	1.471	$0.2 > p > 0.1$	ns
Plastic	$> 4 \leq 6$	5.048	3.518	4.708	$p < 0.001$	sig
	$> 6 \leq 8$	2.691	3.280	0.750	$0.5 > p > 0.2$	ns
	$> 8 \leq 11$	6.049	5.870	0.309	$0.8 > p > 0.5$	ns
Pooling 'Island Top' and 'Causeway' data		Mean height climbed (cm) Polystyrene	Plastic			
	$> 4 \leq 6$	1.878	4.283	8.866	$p < 0.001$	sig
	$> 6 \leq 8$	1.588	2.985	2.751	$0.01 > p > 0.005$	sig
	$> 8 \leq 11$	3.226	5.959	5.865	$p < 0.001$	sig

'Island Top' winkles are insignificant. For each size class, heights climbed on the plastic surface were significantly higher than for the polystyrene surface (Table 10).

Discussion of Results

Upward movement of winkles could be brought about by positive phototaxis or negative geotaxis. Littorina neritoides and Littorina obtusata are usually negatively phototactic and negatively geotactic (Lewis, 1964; Newell, 1970). L.saxatilis (probably L.rudis) has been shown to be negatively phototactic and to respond to plane-polarised light (Charles, 1961). It has been suggested, that if a snail is washed off a rock, or deeply submerged, then these tropisms will guide it up the shore (or rock) and into a dark crevice. But in the absence of crevices, such upshore movement would eventually prove fatal unless checked. Reduced activity which accompanies desiccation has been proposed as a limiting factor for L.obtusata (Barkman, cited in Newell, 1970). In the above experiment, winkles climbed significantly higher on plastic, than on polystyrene. Plastic tends to retain a surface film of water, whereas polystyrene dries out rapidly. Therefore the L.rudis tested appear to behave in a similar way to L.obtusata.

The ability of small 'Causeway' winkles to climb higher, and move readily up the walls of a container, seems to be a real effect, that requires further investigation. Perhaps dramatic differences between populations were not obtained as upward-climbing is an advantageous behaviour strategy in both habitats.

7. CREVICE SEEKING BEHAVIOUR IN WINKLES

Introduction

This experiment, like the previous one, was designed to investigate why 'Causeway' winkles disappeared from the pile at a slower rate than 'Island Top' winkles of the same size. It was hypothesised that 'Causeway' winkles may 'home' to crevices more quickly and more readily than 'Island Top' winkles. Artificial crevices, constructed from polystyrene, were used to test this hypothesis.

Method

As in the previous experiment (10 x 10 x 10 cm) plastic boxes with lids were used. Four boxes were lined with polystyrene ceiling tiles, which had been

Table 11

Summary of results from 'crevice seeking' experiment. For each size class, pooled results from four replicates are shown.

> 4 ≤ 6 mm		Site in experimental environment				
		Floor	Lid	Creviced wall	Plain wall	Totals
'Island Top'	observed	22	46	15	5	88
	expected	18.92	49.68	14.193	5.204	
'Causeway'	observed	18	59	15	6	98
	expected	21.075	55.322	15.80	5.80	
Totals		40	105	30	11	186

$\chi^2_3 = 1.597$; $0.750 > p > 0.500$ ns

> 6 ≤ 8 mm		Floor	Lid	Creviced wall	Plain wall	Totals
'Island Top'	observed	13	36	26	25	100
	expected	23	16.5	25.5	20	
'Causeway'	observed	33	27	25	15	100
	expected	23	16.5	25.5	20	
Totals		46	33	51	40	200
χ^2_1 for each site		8.696	6.682	0.0196	2.50	

$\chi^2_3 = 17.89$; ; $p < 0.001$ sig

> 8 ≤ 11 mm		Floor	Lid	Creviced wall	Plain wall	Totals
'Island Top'	observed	7	20	20	9	56
	expected	12.5	17.5	19.5	6.5	
'Causeway'	observed	18	15	19	4	56
	expected	12.5	17.5	19.5	6.5	
Totals		25	35	39	13	112

$\chi^2_3 = 7.503$; $0.10 > p > 0.05$ ns

cut to size using a heated knife. Holes were cut in two adjacent polystyrene tile walls, using 12.5 mm or 15 mm diameter metal tubes. The large holes were used for large winkles. Since polystyrene tends to dry out (Experiment 6) boxes were filled up with water, to encourage winkles to climb the walls. The outsides of the boxes were covered with aluminium foil to prevent light pnetrating through the walls. The winkles were classified into size categories, as in Experiment 6b. Approximately 20 'Causeway' and 20 'Island Top' winkles of the same size class were placed in each box, and were left overnight (16 hrs.). The following day, winkles on the floor, lid, creviced walls, or plain walls were scored. Four trials were run for each size category. The results were analysed by χ^2 tests.

Discussion of results

Results (Table 11) were somewhat confounded by trends shown in the last experiment. A few of the χ^2 values obtained on analysis of each replicate were significant (see Appendix B) but always as a result of heterogeneity between 'floor' and 'lid'. Results for $> 6, \leqslant 8$ mm winkles (Table 11) reflect this trend. For all size classes tested, differences between numbers of 'Causeway' and 'Island Top' winkles in crevices was not significantly different. Therefore the initial hypothesis is not upheld.

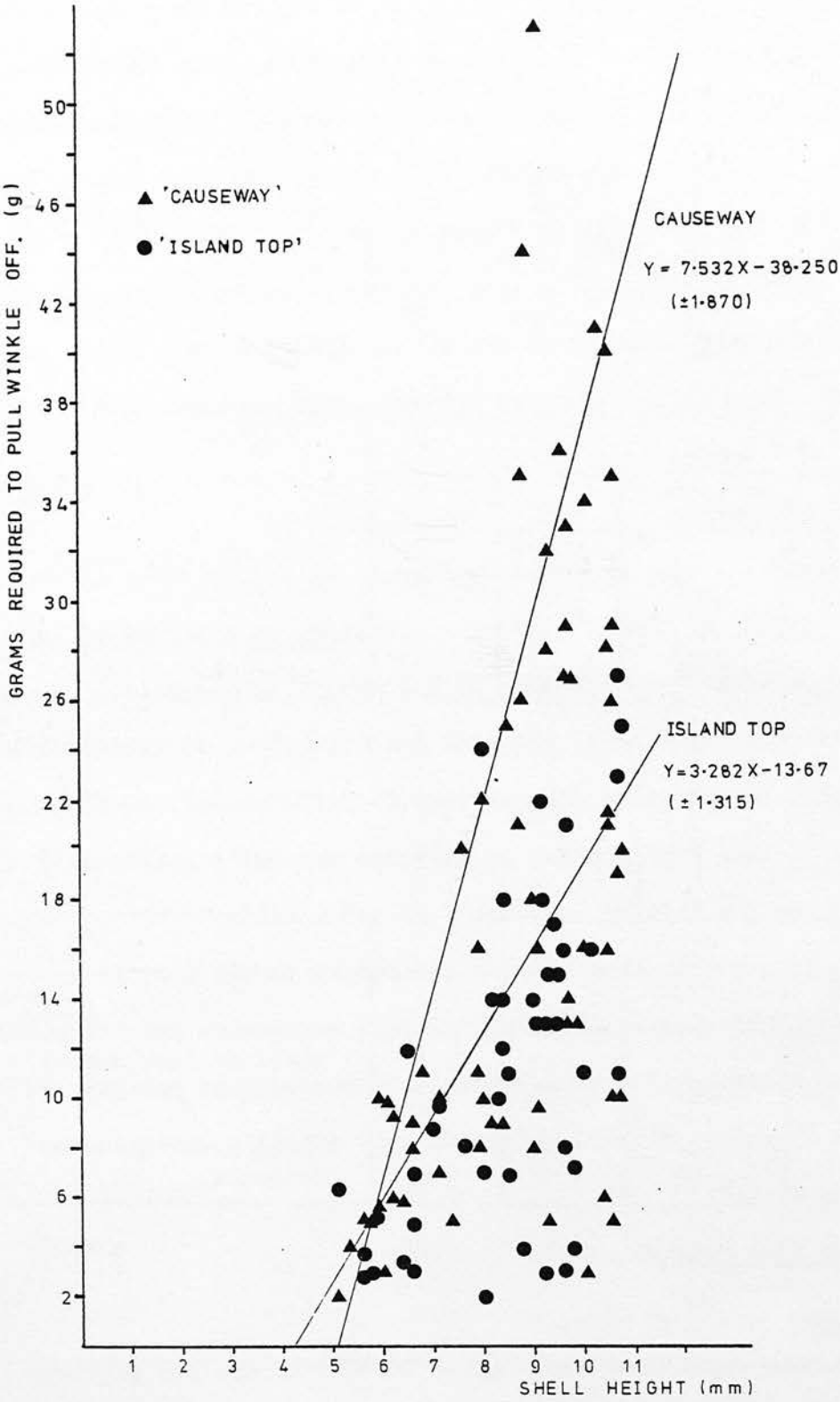
During the experiment, many winkles climbed up to the lid, in an attempt to get out of the sea-water. Perhaps more conclusive results would have been obtained using artificial crevices constructed from perspex, as this would retain a surface film of water and only a little water in the container would be needed.

8. STRENGTH OF THE FOOT MUSCLE

Introduction

The aim of this experiment was similar to that of the two previous experiments; to investigate why 'Causeway' winkles disappeared from the piles at a slower rate than 'Island Top' winkles of the same size (Experiment 4). I also hoped to find some differences between the two populations that could

Fig.10 Force required to pull winkles of different sizes off a glass surface.



Regression lines and equations are obtained by method (a), outlined in the text of experiment 8. 95% confidence limits of b (gradient) are given.

be construed as adaptive. Experiment 2 (Analysis of shell shape) showed that shell shapes of 'Causeway' and 'Island Top' shells are not very different. Therefore, from the shell shapes alone, neither appears to have a larger foot muscle. Nevertheless, a stronger foot muscle for a 'Causeway' winkle would obviously be adaptive, so an experiment was designed to test foot strengths.

Method

'Causeway' and 'Island Top' winkles were divided into size classes ($\geqslant 4$, < 6; $\geqslant 6$, < 9; $\geqslant 9$, $\leqslant 11$ mm), each containing 15 winkles of each type. A synthetic thread tage, about 1 cm long, was attached to the body whorl of each winkle with "Holts 'bond-it' Superglue". All winkles were placed in a large circular glass tank, containing a little sea-water, and left to attach to the walls and floor overnight. Foot strengths were measured in grams using a 10 g or 50 g 'Pesola' spring balance. The spring clip on the balance was attached to the thread tag on a suitable winkle. The winkle was given a slight tap to induce it to hang on firmly. The spring balance was raised slowly, perpendicular to the glass surface. The number of grams required to pull off the winkle was recorded and the shell height measured. 72 'Causeway' and 58 'Island Top' foot strengths were tested. A similar method wa used by Kitching, Muntz and Ebling (1964) for Nucella lapillus.

Results and Discussion

Fig. 10 shows that the force required to pull off a winkle increases with increasing shell height. However, many winkles fall short of the maximum strength possible for each particular size. I analysed this data in two ways.

(a) Results were analysed in a way similar to that of Kitching, Muntz and Ebling (1964). Only the two maximum values (g) for each 0.5 mm size class were considered. For both 'Causeway' and 'Island Top' winkles, these results appeared to increase linearly with shell height. Therefore, the line of best fit was found by regression analysis. Results given in Fig. 10 show that the lines are significantly different, as confidence limits (for the slope) do not overlap. However, both lines cross the X-axis between shell heights of 4 and 6 mm.

Clearly, the lines are not biologically valid for small winkles: an exponential function is more likely. Above a shell height of 6 mm, 'Causeway' L.rudis appear to be able to adhere to a glass surface more firmly than 'Island Top' winkles.

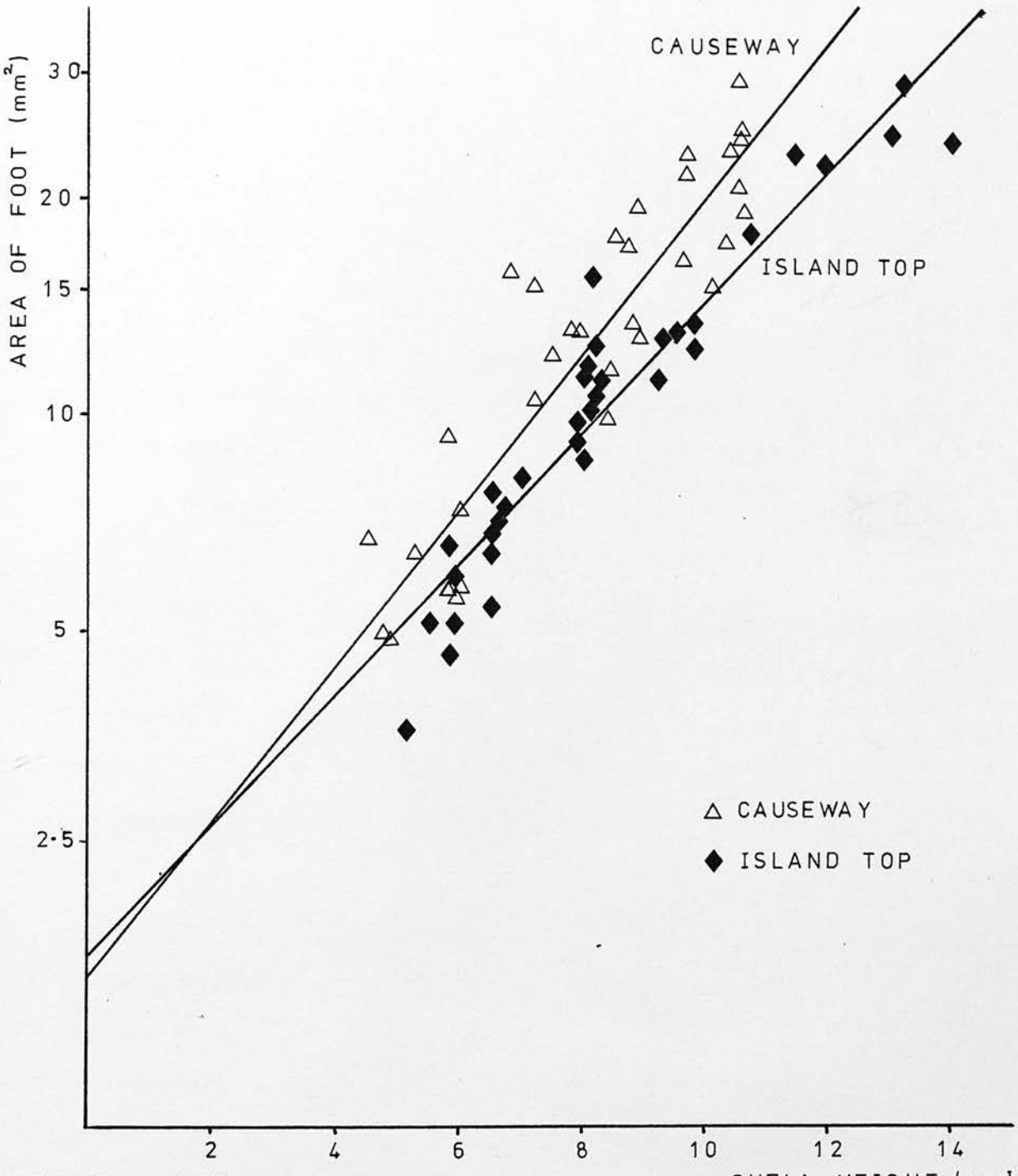
(b) The strength of attachment of the foot is equal to the force exerted per unit area, multiplied by the area of the foot. Since a large winkle has a large foot area, it can exert a greater force than a small winkle. To counter this effect, and to obtain a mean force per unit area typical of 'Causeway' and 'Island Top' winkles, I weighted the above results (g) for each winkle, against the area of its foot (mm^2).

Foot lengths and breadths of individual winkles were measured through glass, using calipers. For each winkle, shell height was also measured. Foot area was estimated by assuming that the foot surface is an oval, (see Appendix C). To eliminate measur ing error, the $\log_e$ of the estimated areas were plotted against shell height, and the lines of best fit calculated. 'Causeway' and 'Island Top' regression lines were not significantly different (see Fig.11). The regression equations were used to accurately predict foot area from shell height. Thus, the force (g) required to pull off each winkle was weighted against predicted foot area (mm). Computed results for 'Causeway' and 'Island Top' animals were analysed using a t-test. Although the mean for 'Causeway' winkles was higher than that for 'Island Top' winkles, results were not significantly different ($t_{117} = 0.363$; $0.8 > p > 0.5$).

Discussion of results

Results show, that if maximum values are considered, (a), the larger 'Causeway' winkles can exert a greater force than 'Island Top' winkles. If all results are analysed (b), there is no difference between populations. It is difficult to tell which of these results is paralleled in nature. Perhaps the force exerted on winkles under natural conditions is a lateral push, rather than being equivalent to a straight pull. Field experiments examining the forces acting on littorinids would probably give interesting results , but would be difficult to do.

Fig.11
Log_e of foot area, plotted against shell height (mm)



Equations of lines

Causeway : $\log_e Y = 0.494 + 0.253 X (\pm 0.0377)$ $t_{33} = 13.72$: $p < 0.05$

Island Top: $\log_e Y = 0.553 + 0.213 X (\pm 0.026)$ $t_{32} = 16.61$: $p < 0.05$

Lines are not significantly different

$F^1_{65} = 3.408$: $p > 0.05$

9. BEHAVIOUR UNDER DESICCATION

Introduction

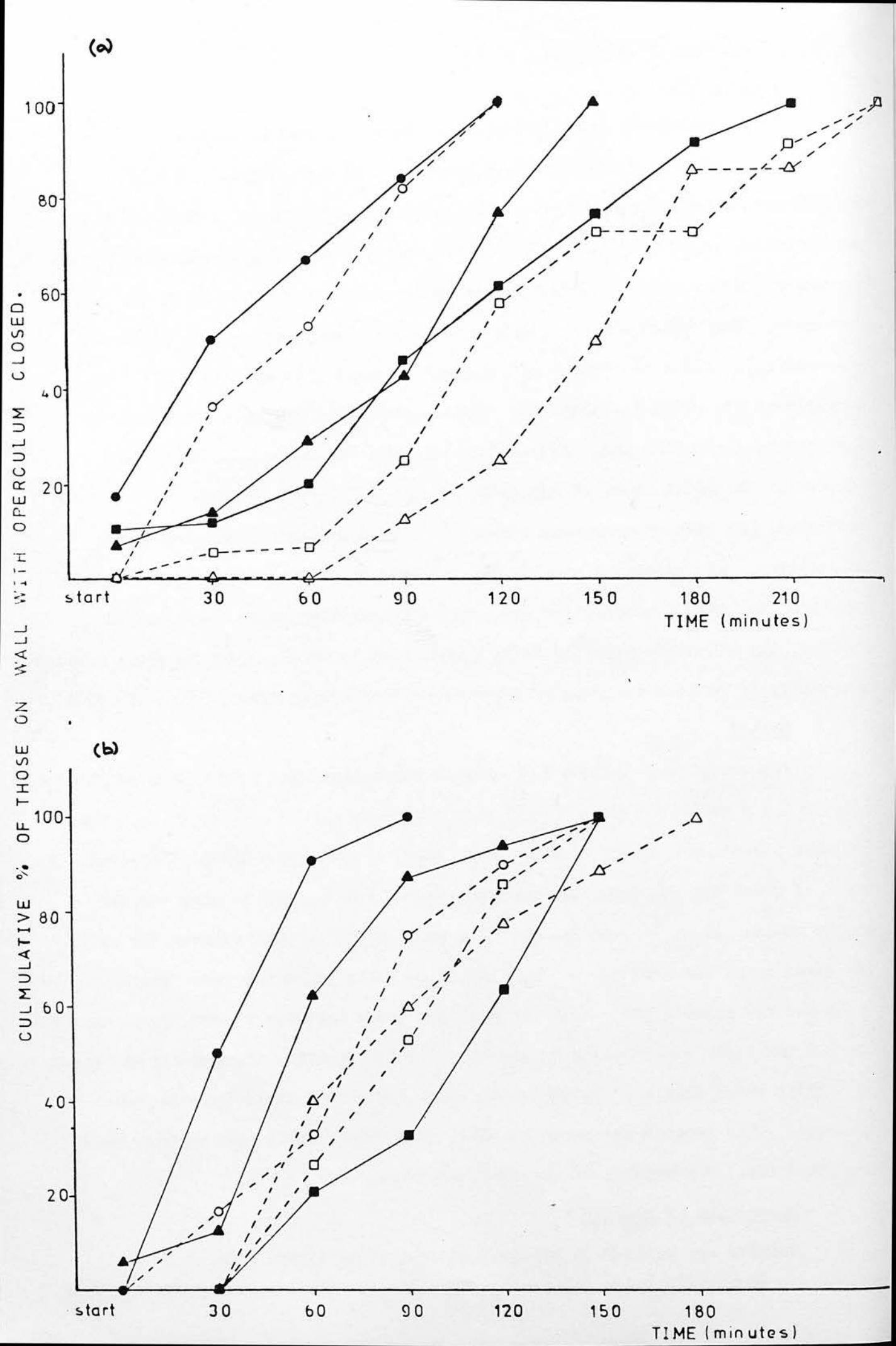
This experiment, and experiment 10, were designed to complement the field experiment on desiccation (experiment 5). It was observed, during maintenance of winkle collections, that, under dry conditions, winkles form a mucous collar round the lip of their shell, retract their foot, and close their operculum. Thus, only a brittle mucous thread attaches the winkle to the substrate. This behaviour is common in the field (Raffaelli, 1976; personal observation). Since the 'Causeway' habitat is dryer than the 'Island' (experiment 5), it is possible that 'Causeway' winkles are better adapted to desiccating conditions than 'Island Top' winkles. Assuming that there is a particular threshold level of humidity, at which an animal closes its operculum, the rate of operculum closure will be a measure of adaptation to desiccation. If 'Causeway' winkles can tolerate dryer conditions than 'Island Top' winkles, then a longer time will elapse before they close their opercula. However, the effect is expected to be complicated by winkle size, as small winkles are likely to be less tolerant of desiccation than larger ones (Raffaelli, 1976).

Method

'Causeway' and 'Island Top' winkles were classified into 1 mm size classes, i.e. $> 4, \leq 5$ mm .... $> 10, \leq 11$ mm) with approximately 10 winkles in each class. All were placed in a large circular glass tank, containing a little sea water. A piece of glass was put over the top, to prevent escapes, and to keep the air inside humid. After 16 hrs, during which many of the winkles climbed the walls, the glass cover was removed, so that the glass walls would dry out. Those win kles which had not climbed the walls, or which had their opercula closed, were removed, counted and their shell height measured. After 30 minutes, the numbers and sizes of winkles which fell off the walls, or which had closed their opercula, were recorded. This process was repeated every 30 minutes, until all winkles were accounted for. The experiment was repeated twice.

Discussion of results

Results are plotted in the form of cumulative curves (fig. 12). χ^2 values are summarised below the graphs. Results for 'Causeway' and 'Island Top'


(a)
100
80
60
40
20
start
30
60
90
120
150
180
210
TIME (minutes)
CULMULATIVE % OF THOSE ON WALL WITH OPERCULUM CLOSED.
(b)
100
80
60
40
20
start
30
60
90
120
150
180
TIME (minutes)

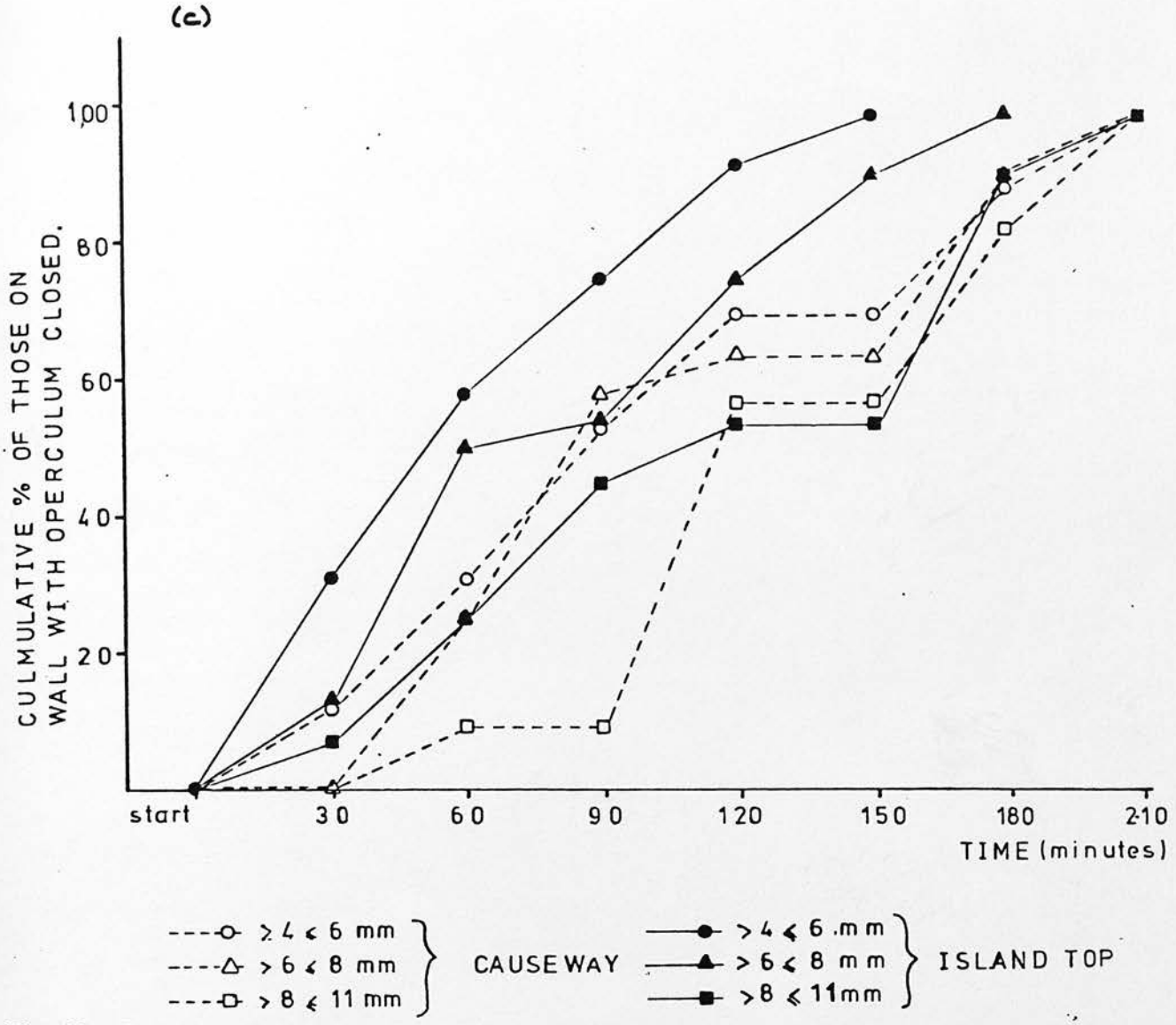


Fig.12 Cumulative totals of winkles with opercula closed graphed against time.

χ^2 values between size classes and populations, are summarised below. Pairs of results not significantly different at the 95% level are bracketed by lines.

	after 1 hour		after 1½ hours	
(a)	'Causeway'	'Island Top'	'Causeway'	'Island Top'
	> 4 ≤ 6	> 4 ≤ 6	> 4 ≤ 6	> 4 ≤ 6
	> 6 ≤ 8	> 6 ≤ 8	> 6 ≤ 8	> 6 ≤ 8
	> 8 ≤ 11	> 8 ≤ 11	> 8 ≤ 11	> 8 ≤ 11
(b)	'Causeway'	'Island Top'	'Causeway'	'Island Top'
	> 4 ≤ 6	> 4 ≤ 6	> 4 ≤ 6	> 4 ≤ 6
	> 6 ≤ 8	> 6 ≤ 8	> 6 ≤ 8	> 6 ≤ 8
	> 8 ≤ 11	> 8 ≤ 11	> 8 ≤ 11	> 8 ≤ 11
(c)	'Causeway'	'Island Top'	'Causeway'	'Island Top'
	> 4 ≤ 6	> 4 ≤ 6	> 4 ≤ 6	> 4 ≤ 6
	> 6 ≤ 8	> 6 ≤ 8	> 6 ≤ 8	> 6 ≤ 8
	> 8 ≤ 11	> 8 ≤ 11	> 8 ≤ 11	> 8 ≤ 11

are significantly different for two out of the six tests made. All graphs show the same trends. Smaller winkles close their opercula after a shorter time than large winkles. The time elapsed before 'Island Top' winkles close their opercula tends to be shorter than for 'Causeway' winkles. These results appear to support the suggestion made in the Introduction, that 'Causeway' winkles are better adapted to desiccating conditions than 'Island Top' winkles.

10. SURVIVAL UNDER DESICCATION

Introduction

This experiment was designed to complement the field experiment on desiccation (experiment 5), and the previous experiment (experiment 9). Since 'Causeway' winkles appear to be less sensitive to desiccation than 'Island Top' winkles, they were expected to survive for longer in dry conditions.

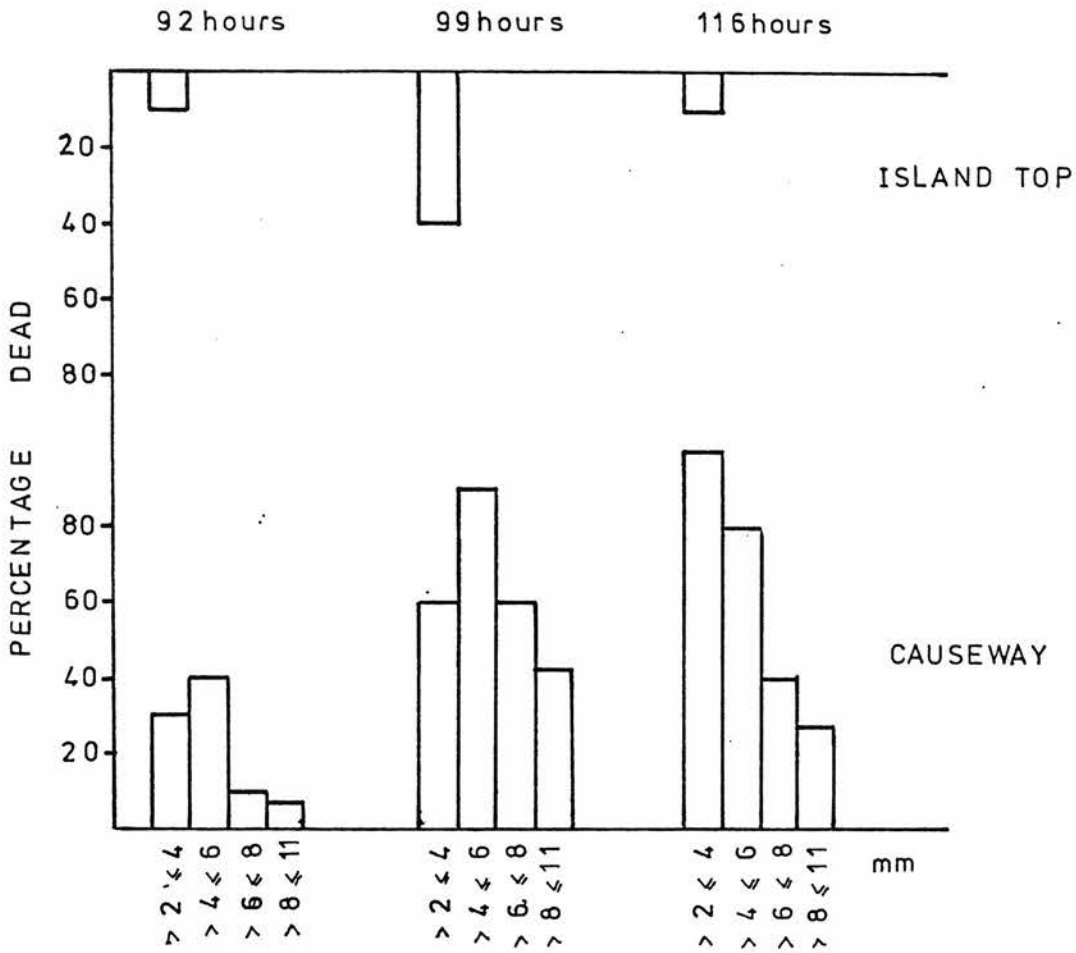
Method

'Causeway' and 'Island Top' L.rudis were each divided into a 'control' and an 'experimental' group. Each group was composed of nine 1 mm size categories (i.e. $> 2, \leq 3$; $> 3, \leq 4$; ..... $> 10, \leq 11$) with 5 winkles in each size class. The two 'experimental' groups were left on the laboratory bench ($\sim 20^{\circ}C$) to dry out. The control groups were placed in small plastic boxes, containing a little sea-water, and covered with a lid. After 4-5 days, (for exact times, see results fig. 13) the experimental groups were placed in sea-water, and allowed to recover for 2 hours. Winkles still alive usually started to crawl around after this time. When survival was in doubt, fine forceps were used to attempt to lift the operculum: if the snail was alive it would draw itself further into its shell, and if dead, the operculum could easily be lifted. The control groups were also checked for dead winkles. The experiment was repeated using two 'Causeway' and two 'Island Top' desiccated groups. A similar method was used by Struhsaker (1968) for Littorina picta.

Discussion of results

Mortality was considerably greater in the 'experimental' groups than the 'control' groups. Among the six control groups, only four deaths, in the 'Causeway' 99 hour group, occurred. Results (fig.13) show that, in all three experiments, 'Causeway' winkles have a significantly higher mortality than 'Island Top'

Fig.13 Ability of various size classes of winkle from each population to withstand periods of desiccation.



χ^2 values between 'Causeway' and Island groups

92 hours	$\chi^2_1 = 7.242$;	$0.01 > p > 0.005$
99 hours	$\chi^2_1 = 26.988$;	$p < 0.005$
116 hours	$\chi^2_1 = 30.527$;	$p < 0.005$

χ^2 values within Causeway group, and between size classes $> 2 \leq 6$ and $> 6 \leq 11$

92 hours	$\chi^2_1 = 4.47$;	$p < 0.05$
99 hours	$\chi^2_1 = 7.410$;	$p < 0.01$
116 hours	$\chi^2_1 = 8.961$;	$p < 0.005$

winkles. Smaller 'Causeway' winkles ($> 2, \leq 6$ mm) are significantly more affected by desiccation than larger animals ($> 6 \leq 11$ mm) (see Fig.13). Therefore, although 'Causeway' winkles appear to be less sensitive to dry conditions in the short term (Experiment 9) they cannot tolerate desiccation over a long period.

The habitat of the 'Island Top' winkles is between high water neap tide level, and high water spring tide level (see fig.2). For 4-5 days out of the 14 day cycle, this habitat is not covered by water. Selection for tolerating 4-5 days of dry conditions must have occurred. Nevertheless, a few of the smallest winkles die as a result of dry conditions. Probably, the changes in size structure in this population, between February and March (fig. 3) are due to increased mortality among smaller winkles as a result of dryer weather conditions.

Most 'Causeway' winkles are covered by water at all high tides. Even if some winkles find themselves above the water mark, migration vertically down the pile would be relatively easy. If winkle mobility is exceedingly low, toleration to long periods of desiccation is expected to be correlated with height found on pile. Since 'Causeway' winkles can usually rely on being covered by water at each tide, there will be selection only for short term resistance to desiccation.

11. REPRODUCTION EXPERIMENT

Introduction

The aim of this experiment was to attempt to relate the life-history tactic of each population to the particular selection pressures found important in the field and behaviour experiments. Various aspects of reproduction were measured for each habitat, namely: number of young; weight of individual young; size at maturity; male-female ratio, and reproductive effort. The prevalence of parasitism was also noted. Size at maturity was estimated as the shell height of the smallest male found, with a fully developed penis (after Faller-Fritsch, 1977).

Reproductive effort can be defined as the proportion of resources diverted to reproduction, summed over the time interval in question (Hirshfield and Tinkle, 1975). I estimated reproductive effort as:

$$\frac{\text{weight of one young} \times \text{total number of young}}{\text{weight of mother}}$$

Ideally, the above estimate should be in terms of calories, rather than weight.

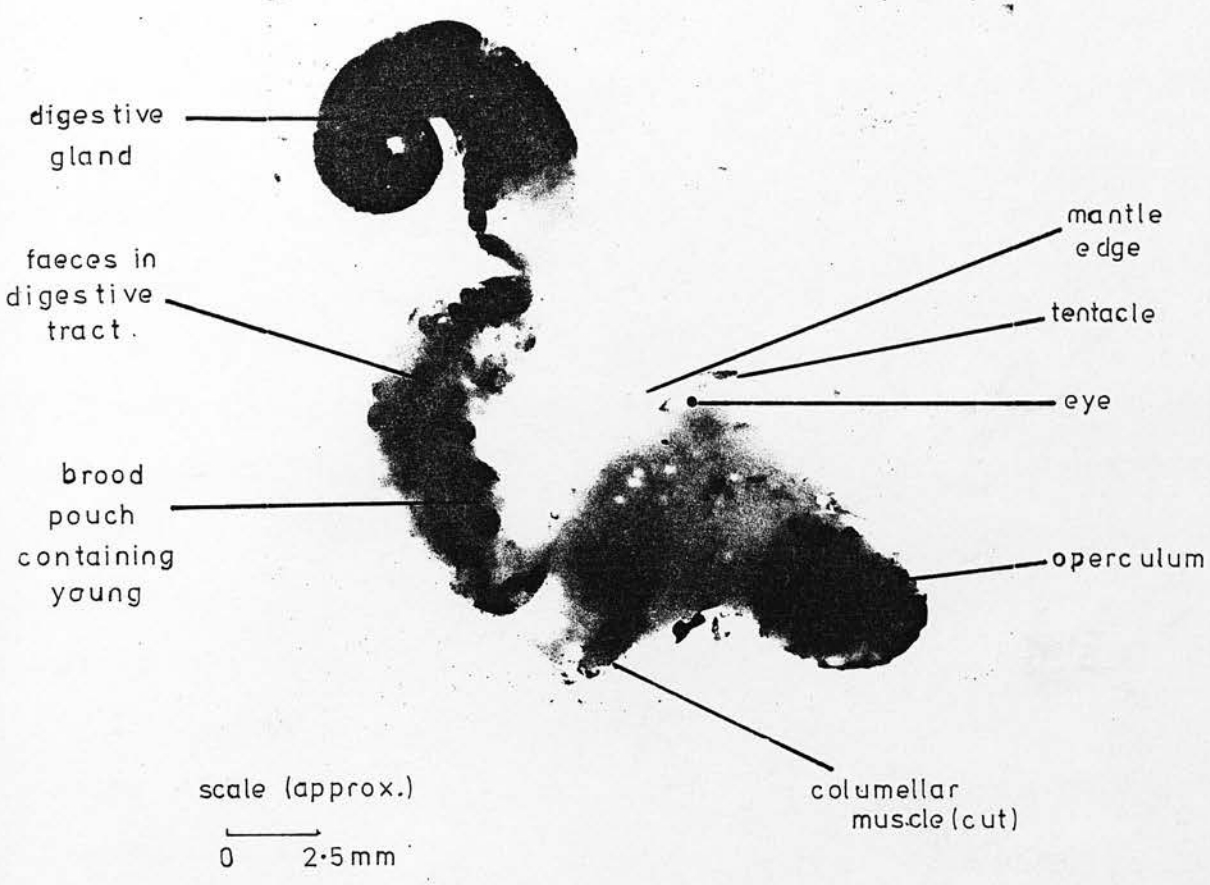


Plate 8. L.rudis removed from its shell and seen from the right side.

Also, no account is taken of the time required to accumulate the energy necessary for reproduction. For example, winkles in one population may produce a given number of young twice as fast as winkles in another population. Clearly, the first population must accumulate energy faster, and have a higher reproductive effort than the second, yet my formula overlooks this. Nevertheless, it was the best I could do in the time available.

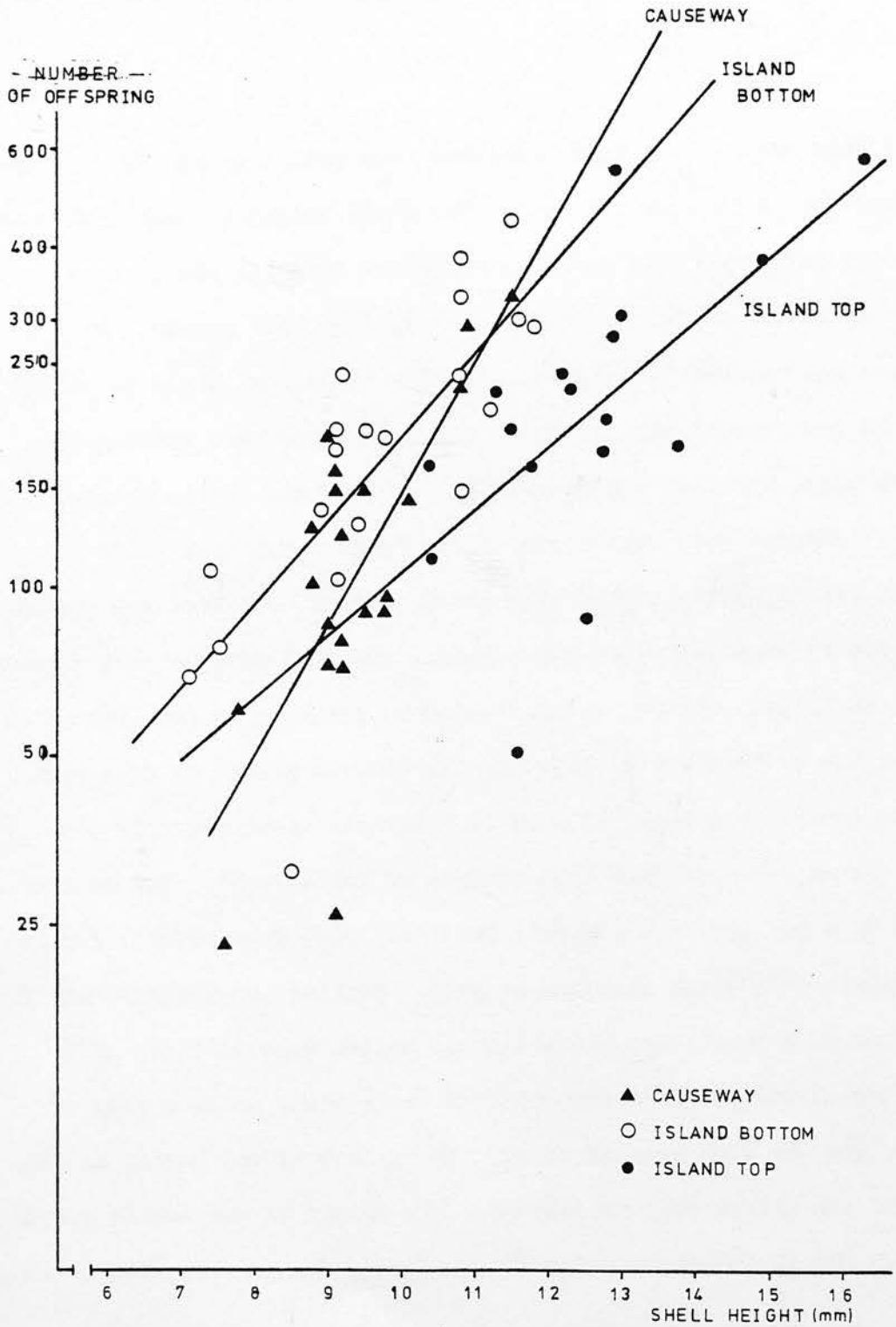
Method

Winkles from each of the three habitats were collected on the 11th and 26th January, and stored in a deep freeze. The shell height of each winkle was measured with dial calipers. The animal was removed from its shell, by inserting a scissor blade in the aperture, and cutting along the shell groove. When the columellar muscle was reached, it was cut, so that the animal could be pulled gently out of the rest of its shell. The snail was placed in a watch-glass filled with sea-water, examined for parasitism, and its sex (male, female, juvenile) noted. Embryos were teased out of the brood pouch (see plate 8) of unparasitised femles, using a pair of mounted needles. Shelled and unshelled embryos (see plate 9) were separated and counted. Shelled embryos were pipetted into a watch-glass filled with tap water, to remove traces of salt. The water was drained from the watch-glass by pipette, the embryos picked up on a clean finger, and transferred to a small (1.5 cm in diameter) aluminium foil dish. Aluminium foil dishes were prepared from squares of 'Alcanfoil'. The embryo batch was dried in a hot air oven ('Sunvic Controls Ltd.' Type F102/3) for 24 hours. (Time required to reach constant weight). Shelled embryos in their foil dish, were weighed on a 'Oertling' microbalance, to the nearest tenth of a milligram. The dried embryos were removed from their dish, using a pair of mounted needles, and the dish weighed alone. The weight of the batch, and the average weight of one embryo were calculated. The weight of the mother could be estimated from the shell height using the following formula (supplied by Atkinson, unpubl. data):

$$y = 0.05\ x^{2.59}$$ when y = dry weight (mg)
x = shell height (mm)

The experiment was repeated until about 20 mature females from each habitat had been dissected.

Fig. 14 Numbers of offspring produced by winkles of different sizes from each population.



Equations of lines:

Causeway : $\log_e Y = -0.3998 + 0.5405 \text{ X } (\pm 0.229)$; $t_{19} = 4.9106$: $p < 0.05$

Island Bottom: $\log_e Y = 1.783 + 0.345 \text{ X } (\pm 0.138)$; $t_{18} = 5.243$: $p < 0.05$

Island Top : $\log_e Y = 2.079 + 0.259 \text{ X } (\pm 0.178)$; $t_{15} = 3.106$: $p < 0.05$

Discussion of results

Size at Maturity

Results (Table 12) show that 'Causeway' and 'Island Bottom' winkles reproduce at a much smaller size than 'Island Top' winkles. However, only the size given for 'Island Top' winkles is reliable, as lack of time prevented me from carrying out a full investigation. Sizes at maturity for 'Causeway' and 'Island Bottom' winkles are likely to be lower than those given.

Weight of one embryo

Results (Table 12) were analysed using a one-way analysis of variance, and a Student-Newman-Keuls test. 'Island Top' winkles produce the largest young, 'Causeway' winkles the next largest and 'Island Bottom' the smallest. Young do not increase in weight with increasing size of mother ($t_{15} = 0.3076$, $t_{19} = 0.8082$, $t_{18} = 1.95$; $p > 0.05$ for all).

Number of embryos produced

Number of embryos produced was found to increase exponentially with size of mother. Therefore the size of mother (mm) was plotted against $\log_e$ number of offspring, for each habitat, and regression lines calculated (see fig. 14). The gradients and intercepts at the y-axis, of the three lines are not significantly different (for gradients; $F^2_{52} = 2.794$; $0.1 > p > 0.05$, for intercepts; confidence limits overlap: methods in Sokal and Rohlf, 1970 pp 450 and 424). However, since gradients are very nearly significant, a larger sample size would probably give significant differences.

Reproductive effort

When the mean reproductive effort is calculated for each population (Table 12) the 'Island Top' mean is greatest. However, if results are plotted on a graph (fig. 15) and regression lines calculated, then reproductive effort increases linearly with shell height for 'Causeway' and 'Island Bottom' winkles but not for 'Island Top' winkles. The 'Causeway' regression line is not significantly different from the 'Island Bottom' line ($p > 0.10$: method in Sokal and Rohlf, 1970, p.450). Thirteen of the seventeen 'Island Top' results are below the 'Causeway' regression line, showing that, for equivalent shell heights 'Island Top' reproductive effort is generally lower than that of 'Causeway' winkles, ($p = 0.0245$: from binomial distribution).

Table 12

Summary of measurements on aspects of reproduction

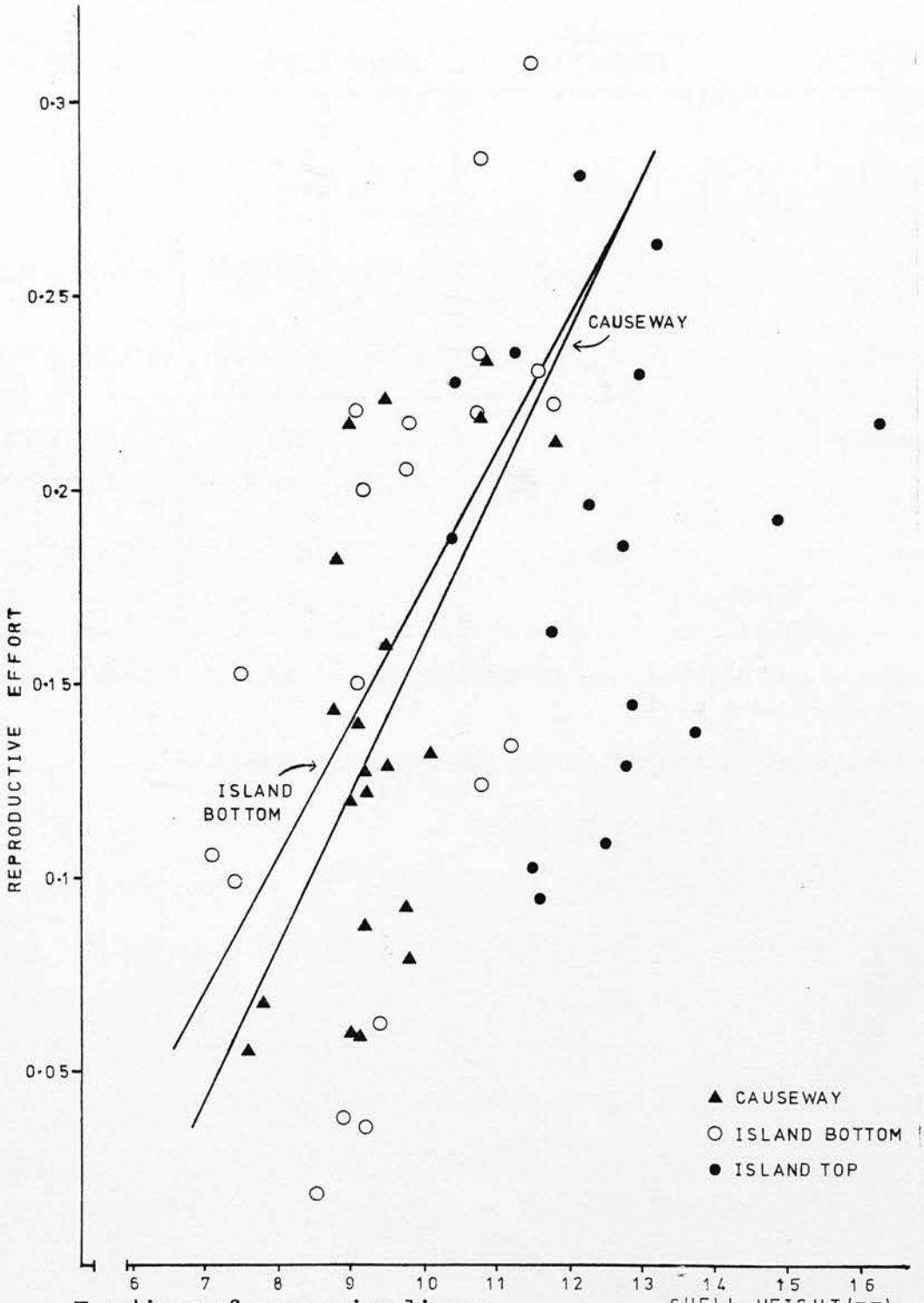
	ISLAND TOP	ISLAND BOTTOM	CAUSEWAY
Number measured	17	20	21
Shell height at maturity (mm)	9.7	< 7.1	< 5.5
Mean weight of 1 shelled embryo (mg)	0.0309 ± 0.00475	0.0152 ± 0.00288	0.0196 ± 0.00244
Mean reproductive effort	0.0182 ± 0.0291	0.163 ± 0.0400	0.136 ± 0.02706
Male:Female ratio	19 : 19	4 : 22	17 : 21
χ^2_1 value	0 ; $p > 0.05$	11.714 ; $p < 0.001$	0.421 ; $p > 0.05$
% parasitised	32.05	7.143	3.380

χ^2_2 between = 22.189; $p < 0.05$

Weights of embryos and reproductive effort analysed by Analysis of variance and Student-Newman-Keuls test.

Means not significantly different at the 95% level are underlined.

Fig. 15 Reproductive effort of winkles of different sizes from each population



Equations of regression lines:

Causeway : $Y = -0.233 + 0.0394 X (\pm 0.0247)$ $t_{19} = 3.332$; $p < 0.05$

Island Bottom : $Y = -0.174 + 0.0348 X (\pm 0.0242)$ $t_{18} = 3.018$; $p < 0.05$

Island Top : line not significant $t_{15} = 0.275$ $p > 0.05$

Causeway and Island Bottom lines are not significantly different

$F^{1}_{39} = 0.08546$; $p > 0.10$

Male/Female Ratio

Results (Table 12) show that the male:female ratio in the 'Causeway' and 'Island Top' populations, does not differ significantly from a 1:1 ratio ($\chi^2_1 = 0.2$; $\chi^2_1 = 0$; $p > 0.05$ for both). 'Causeway' results, however, are not reliable, as L.arcana males could not be differentiated from L.rudis males. Many more females than males are found in the 'Island Bottom' population ($\chi^2_1 = 11.714$; $p < 0.001$). This result assumes that the animals dissected were a random sample. If males and femles have behaviour differences, such that males tend to be found deeper inside crevices between mussel shells, then sampling will be biased in favour of females. If males tend to be smaller than females, this effect will be reinforced.

Prevalence of parasitism

The 'Island Top' population shows a much higher rate of parasitism than 'Causeway' or 'Island Bottom' populations (see Table 12). In nine of the parasitised winkles, the cercarial parasite Microphallus similis (Jägerskiöld) was identified (Method and Key in James, 1968). The cercariae of this parasite leave L.rudis and penetrate the shore crab (Carcinus maenus) by way of the gill chambers. Metacercaria develop inside the crab, and when eaten by a gull or tern the parasite reaches its adult stage. Egg in the bird's faeces are picked up by the the snail to complete the cycle (Stunkard, 1957).

In all of the larger snails examined, parasitism had resulted in castration. James (1965) examining other digenean parasites of L.saxatilis, concluded that castration is caused by the growing sporocysts compressing germinal tubules. Probably, Microphallus similis acts in the same way. The castrating effect of the parasites studied by James (1965) was thought to be minimal, as reproductively 'spent' hosts are often affected. However, most of the parasitised winkles found in this study, were between 9 and 11 mm in shell height, which is the beginning of their reproductive life. Therefore, parasitism seems to be an important selection pressure.

Plate 9. Contents of a brood pouch, showing young at different developmental stages. 0 ——— (approx) 1 mm

GENERAL DISCUSSION

In this section, I will discuss the selection pressures acting on each population, and the way in which the winkles respond to these forces, particularly in relation to their life-history strategies. I will consider results obtained from other L.rudis populations, and compare them to my own. For the sake of comparison, cliff populations, with their small crevices, and often high degree of exposure, are taken to be analogous with the 'Causeway' population.

'Causeway' population

The principle selection pressures here are dislodgement by wave-action, and desiccation. Dislodgement is not size specific. This result is in marked contrast to the work of Emson and Faller-Fritsch (1976) and Raffaelli and Hughes (1978) who found that the maximum size of L.rudis on exposed cliff faces was determined by crevice width, and implied that winkles too large to fit crevices were washed off. The reason for the differences in results may be that barnacle crevices provide less protection for small winkles than rock crevices, yet have identations suitable for large winkles that are not found on a smooth rock face. However, for Nucella lapillus, Kitching et al (1964), in an experiment similar to mine (Experiment 4), found no correlation between survival and shell height.

Desiccation on the Causeway is severe between tides. 'Causeway' winkles appear to be physiologically adapted to short periods of desiccation, as a relatively long time elapses before they let go with their feet, close their opercula, and hang by a mucous thread. Obviously, an animal attached to the pile by its foot is much less likely to fall off, or to be washed off by the rising tide. Small winkles tend to be less tolerant of desiccation than large winkles. These results are paralleled by those of Davies (1969) for Patella vulgata. High level Patella are better able to limit the rate of water loss than low level animals. Survival on desiccation is proportional to the percent of body water lost, therefore, small Patella survive less well than large ones.

'Causeway' mortality appears to be extremely high, due to desiccation when the tide is out, and wave-action when the tide is in. The probability of death increases, the longer the winkle remains on the pile. It is, therefore, advantageou to reproduce as early as possible. However, the larger a winkle is, the more

young it can produce. The strategy that each winkle adopts is to increase diversion of resources to reproduction with increasing size. Increasing reproductive effort with age is predicted by some life-history theory (e.g. Pianka and Parker, 1975; Stearns, 1976). A high reproductive effort is generally correlated with low survival (Pianka, 1976; Stearns, 1976; Horn, cited in Krebs and Davies, 1978). The low survival under desiccation of 'Causeway' winkles, compared with 'Island Top' winkles, supports this correlation.

Young will tend to be of the smallest size necessary for survival, so that the maximum number can be produced for a given reproductive effort. The particular size of young will depend on the exact shape of the animal's survivorship curve. 'Causeway' winkles produce medium size young, with respect to 'Island Bottom' and 'Island Top' animals. There are two reasons why offspring are of this size. Firstly, 'Causeway' young may be heavier than 'Island Bottom' young, as they require to have some resistance to desiccation. Secondly, if new born young suffer similar mortality to larger winkles, then large offspring will have an advantage over smaller ones,as they will require less growing time to reach sexual maturity.

Faller-Fritsch (1977) studying a population of L.rudis on an exposed, stable boulder shore found that size of maturation was small and that embryos produced were small. The weights of these embryos are similar to those of the 'Causeway' embryos.

At many of the exposed cliff sites studied by Raffaelli (1976), mean female size was small, maturation early, and embryo size large (compared to boulder shores). He suggested that these populations are regulated by density dependent factors, and that large embryo sizes are an adaptation to high levels of competition. He implies that these winkles are 'K strategists'.

Classical 'K selection' (Pianka, 1970) takes place in relatively stable environments, where the number of animals is near 'carrying capacity'. Animals are resource limited, therefore selection favours those that can cope with competition and crowding Characteristics of 'K' strategist are large size, late maturity and production of small numbers of large young (McArthur and Wilson, 1967). The only 'K' characteristics consistent with Raffaelli's population

is large embryo size. On exposed, stable boulder shores, the limiting resource is availablity of crevices (Emson and Faller-Fritsch, 1976). Since large crevices are suitable for both large and small winkles, but large winkles can only fit in large crevices, population limitation will affect larger winkles most. Classical 'K' selection requires that juvenile mortality is higher than adult mortality (Wilson, 1975). Therefore, unless adult winkles or territories in the manner of the limpet, Lottia gigantea (Stimson, 1973), adult mortality will be greater than juvenile mortality, and 'K selection' will break down. Possibly, the reasons for the sizes of young born to 'Causeway' winkles are also applicable to Raffaelli's populations.

'Causeway winkles' are composed of L.rudis and about 30% of L.arcana. I assumed that both species would show similar adaptations to physical conditions experienced on the 'Causeway'. Since the density of winkles on the 'Causeway' piles appears to be high, it is likely that L.rudis and L.arcana are competing with each other. Further work on competition between these two species would be interesting.

'Island Top' population

Selection pressures important here are desiccation, wave action, and perhaps crab predation and parasitism.

Short term desiccation is not so severe in the 'Island Top' habitat as the 'Causeway' habitat, as in dry weather animals can take refuge under stones and overhangs. Movement off large boulders, in dry conditions, has also been observed from the top-shell, Monodonta lineata. Courtney (1972) noticed that the number of M.lineata on boulders decreased with increasing wind speed. He attributed movement into shelter as protection against desiccation. 'Island Top' winkles close their opercula more readily than 'Causeway' winkles, indicating a lower tolerance to desiccation. However, long term survival under desiccation is higher than that of 'Causeway' winkles, especially among the large animals. Perhaps the two are inversely correlated. An animal with its operculum closed cannot feed. Possibly, the lowered reproduction during the summer months (Berry, 1961) is a result of less feeding time.

Crushing by boulders and crab predation are probable selection pressures on boulder shores (Raffaelli, 1977). Size distribution curves seem to indicate that winkles greater than 1 cm suffer a lower mortality than smaller winkles. The shell thickens as it grows , (Raffaelli, 1977; personal observation) therefore these large winkles are perhaps able to withstand most crushing and predation. Ebling et al (1964) have shown that large Nucella lapillus are more resistant to crab predation than small individuals. Hughes and Elner (1979), working on the same animal, have obtained similar results. 'Island Top' individuals show a distinctive behaviour pattern, perhaps as a response to predation. When winkles adhering to the sides of boulders are touched with forceps, or if their boulder is moved, they let go with their foot, drop off, and disappear among the stones (field observation). This behaviour is not exhibited by 'Island Bottom' or 'Causeway' winkles.

The high levels of parasitism in the 'Island Top' habitat indicate that large numbers of gulls are present, and suggest that crab predation might occur. Parasitism may affect behaviour, as Williams and Ellis (1975) have shown that migration of Littorina littorea parasitised with Cryptocotyle lingua is impaired.

'Island Top' winkles produce heavier young, mature at a larger size, and have a lower (relative) reproductive effort than the other populations. Similar reproductive tactics have been reported for a boulder shore population studied by Faller-Fritsch (1977). He suggested that large young are less susceptible to crushing, burial and desiccation. Small L.rudis appear to divert resources to growth, rather than reproduction, so that the period when crushing or predation is likely, is as short as possible. The large number of young produced by 'Island Top' L.rudis may be required because of high mortality rates among juveniles. A large proportion of young may succumb to desiccation, parasitism or predation by birds or crabs, before they reach sexual maturity.

Because reproduction is generally associated with a 'cost' in terms of survival, the 'Island Top' winkles, with their low reproductive effort, might be expected to survive longer as breeding adults than 'Causeway' winkles. Producing young over a long period of time, will ensure that some are born into a

favourable environment.

These predictions are largely speculative, and could only be justified by further experimentation on this population.

Many of the boulder-shore populations studied by Raffaelli (1976), were composed of individuals which matured at a large size and produced many small offspring. He proposed that selection is density independent, thus implying that these populations are 'r selected'.

Pure 'r selection' occurs in a variable or uncertain environment, where there is high and catastrophic mortality, so that the population never reaches 'carrying capacity' (Pianka, 1970). Small size, early maturity, and production of large numbers of small young are characteristic of an 'r strategis However, Raffaelli's populations are composed of large individuals that mature late. Thus his populations are not explained adequately by 'r selection'. The explanation similar to that put forward for my 'Island Top' population, can probably account for the characteristics of Raffaelli's animals. Differences in sizes of young are perhaps related to the particular stability of the boulders and stones in the site studied.

Island Bottom population

Selection pressures acting on this population are presumed to be wave-action, crab predation, and entrapment by the byssus threads of mussels. The size of young is small, and reproductive effort increases in a similar way to that of the 'Causeway' winkles.

Many 'Island Bottom' individuals have been observed with some byssus threads attached to their shell. On the shore, winkles have been found completely enmeshed by threads. More work is required on this interesting and unusual selection pressure.

The 'Island Bottom' habitat consists of groups of boulders isolated by stretches of sand (plate 4). Perhaps production of large numbers of small young facilitates colonisation of new boulders. As reproductive effort increases with size, it can be predicted that mortality increases with age, perhaps in a similarly dramatic way to that of the 'Causeway' winkles.

Many more females than males are found in the 'Island Bottom' population. The sex-ratio could be a result of sampling error, or environmental sex determination (e.g. in fish: Harrington, R.W. in Reinboth, 1975). Alternatively, this characteristic could be linked with colonising ability, as in the wood lemming Myopus schisticolor, which appears to have an X-linked male suppressing gene (Fredga et al., 1976).

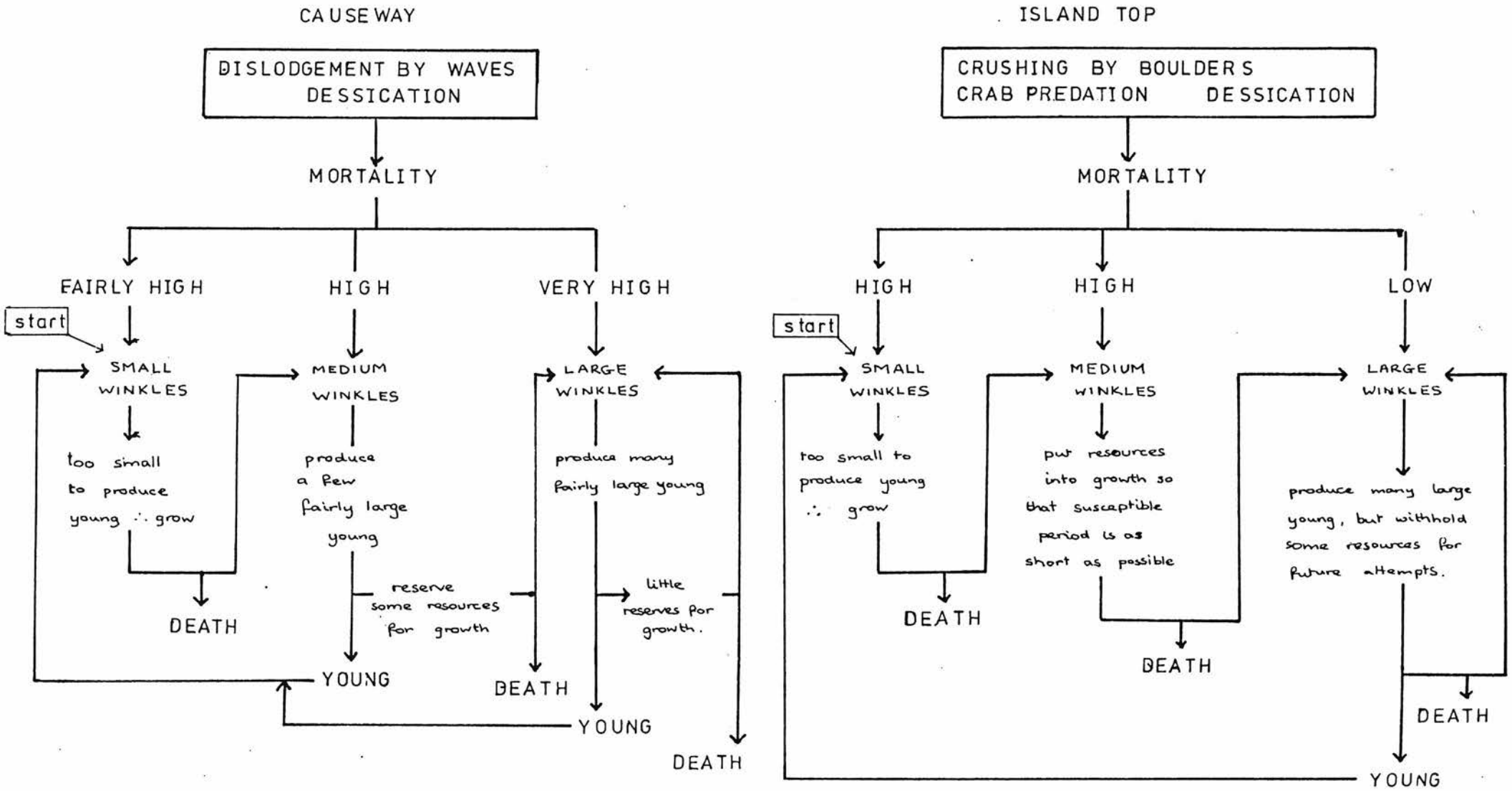
Further investigation of this interesting population would probably prove rewarding.

The differences between populations may be environmental or genetic in origin. Shell colour polymorphisms are generally assumed to have a genetic basis (Pettit, cited in Raffaelli, 1979b). 'Causeway' L.rudis are more variable in colour than the Island populations; this may indicate a genetic difference. It is possible that characteristics such as resistance to desiccation, size at maturation, and embryo size, are also under genetic influence. By transferring winkles from one site to another, Berry (1961) showed that winkles rapidly acquired the characteristic number of embryos of the site to which they were transferred. This significant environmental effect could be further investigated by extending Berry's experiment to include measurements of embryo size, reproductive effort, and age at maturity.

It is apparent, from all the studies done, that L.rudis is remarkably adaptable to local conditions. Each population appears to reflect the particular selection pressures acting upon it. The varying reproductive tactics of L.rudis populations, cannot be adequately explained by 'r' and 'K' selection. L.rudis is not alone in this respect: the green turtle (Chelonia mydas), for example, is large and reproduces repeatedly, yet produces very many small young. This, and other animals not conforming to 'r' and 'K' selection are given in Wilbur, Tinkle and Collins (1974) and Atkinson (1979).

The 'r' and 'K' selection labels which have been associated with many animals to describe their reproduction can provide a very general picture of the animals life-style, but often do not explain it adequately. A theoretical alternative to 'r' and 'K' selection is based on the relative effects of adult and juvenile mortality (Murphy, 1968; Schaffer, 1974; Stearns, 1976).

Fig. 16. Simplified diagram showing possible relationships between life-history tactics and selection pressures.



If a fluctuating environment has most impact on adult mortality, then increased reproductive effort, large clutches and short-lived organisms are favoured. Environmental variability that adversely effects juvenile survival selects for reduced reproductive effort, small clutches, and longer lived organisms, so that at least some clutches are born into a favourable environment. However, Hirshfield and Tinkle (1975) point out that lower effort alone cannot be favoured, unless increased juvenile survivorship results. Where predation on young is high, as for the green turtle, a large clutch is required to 'satiate' the predators even in a favourable year.

It appears to me, than an animal's life-history tactic can only be fully explained by investigating the particular selection pressures acting upon it. Since the reproductive tactic of an individual determines how many gene copies will be passed onto the next generation, it can be expected that the selected strategy will be that which most effectively counters the particular environmental and biotic regulating factors of its habitat. I think that no satisfactory general life-history theory will be able to deal with all probable mortality factors. However, theory which deals with parts of an animal's reproductive tactic, e.g. clutch size, size of young, and size at maturity provide useful and applicable concepts.

In conclusion, I can propose a tentative 'life-history tactic' model for the 'Causeway' and 'Island Top' populations (Fig. 16), and include the selection pressures important to each one. Further work is required to verify these models. In particular, experiments to confirm the suggested mortality factors of the 'Island Top' population, and to test the assumptions of my measure of reproductive effort, would be valuable. The ability of L.rudis to respond to very local changes in selection pressures, makes it an ideal animal for studying aspects of micro-evolution. I feel I have only scratched the surface of a highly interesting investigation.

SUMMARY

1. Selection pressures acting on three populations of the winkle Littorina rudis were investigated, in order to determine the reasons for their different characteristics.
2. The effect of dislodgement by wave action on a population living among barnacles was severe, and not size specific.
3. Desiccation was more intense in the above population, than for a population living high up on a boulder shore. The former population appeared to be better adapted to short-term dry conditions, but less able to survive long-term desiccation, than the latter.
4. Aspects of the reproductive strategies of each of the three populations were measured, and related to the selection pressures found.
5. Reproductive tactics of each population were examined in the light of current life-history theory.

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APPENDIX A

Two way-analysis of variance table between size-class and winkle type used in Experiment 6a.

Anova Table

	df	SS	MS
Between size classes	5	9.05	1.81
Between populations	1	10.97	10.97
Interaction	5	8.39	1.678
Error	36	108.73	3.020
	47	137.14	

$F^{5}_{36} = \frac{1.678}{3.020} = 0.555$; $p > 0.05$ $\therefore$ pooled with 'Interaction'

Between populations $F^{1}_{41} = \frac{10.47}{2.865} = 3.806$; $0.10 > p > 0.05$

Between size classes $F^{5}_{41} = \frac{1.81}{2.856} = 0.633$; $p > 0.05$

APPENDIX B

Table showing results of each replicate for Experiment 7.

$> 4 \leqslant 6$

	Floor	Lid	Crevices	Plain walls	Total
(a) Island Top	9	12	1	1	23
Causeway	7	12	3	2	24
	16	24	4	3	47

$\chi^2_3 = 1.615$; $0.75 > p > 0.500$ ns

(b) Island Top	2	11	7	1	21
Causeway	3	12	8	2	25
	5	23	15	3	46

$\chi^2_3 = 0.298$ $0.975 > p > 0.900$ ns

(c) Island Top	3	12	5	1	21
Causeway	0	21	2	2	25
	3	33	7	3	46

$\chi^2_3 = 6.778$ $0.10 > p > 0.05$ ns

(d) Island Top	8	11	2	2	23
Causeway	8	14	2	0	24
	16	25	4	2	47

$\chi^2_3 = 2.338$ $0.75 > p > 0.5$ ns

$> 6 \leqslant 8$

(a) Island Top	6	9	5	5	25
Causeway	13	8	3	1	25
	19	17	8	6	50

$\chi^2_3 = 5.80$ $0.25 > p > 0.10$

(b) Island Top	1	13	7	4	25
Causeway	9	8	5	3	25
	10	21	12	7	50

$\chi^2_3 = 8.066$ $0.05 > p > 0.025$

(c) Island Top	2	9	6	8	25
Causeway	5	9	7	4	25
	7	18	13	12	50

$\chi^2_3 = 2.696$ $0.5 > p > 0.25$

(d) Island Top	4	5	8	8	25
Causeway	6	2	10	7	25
	10	7	18	15	50

$\chi^2_3 = 1.975$ $0.750 > p > 0.50$

APPENDIX B - cont'd

> 8 ⩽ 11

	Floor	Lid	Crevices	Plain walls	Total
(a) Island Top	1	1	3	3	8
Causeway	5	1	2	0	8
	6	2	5	3	16
(b) Island Top	-	1	5	2	8
Causeway	2	-	6	-	8
	2	1	11	2	16

pooled a and b χ^2_3 = 10.0; 0.025 > p > 0.010 sig

(c) Island Top	5	2	10	3	20
Causeway	5	6	7	2	20
	10	8	17	5	40

χ^2_3 = 2.729; 0.500 > p > 0.250 ns

(d) Island Top	1	16	2	1	20
Causeway	6	8	4	2	20
	7	24	6	3	40

χ^2_3 = 6.571 0.10 > p > 0.05 ns

APPENDIX C

Equation for area of oval used in experiment 8.

A circle is a special case of an oval

$$\text{Area of oval} = \left(\frac{1/2d_1 + 1/2d_2}{2}\right)^2 \pi = 1/4\,(d_1 + d_2)^2 \pi$$

$$= 1/16\,(d_1 + d_2)^2 \pi$$